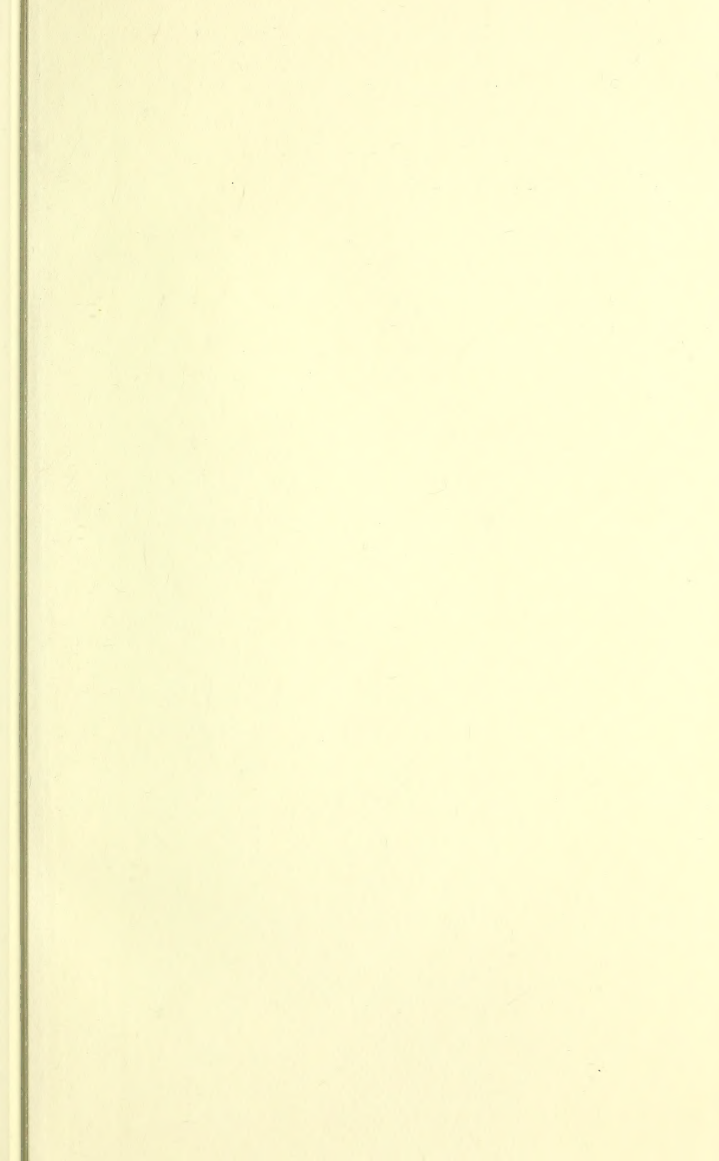





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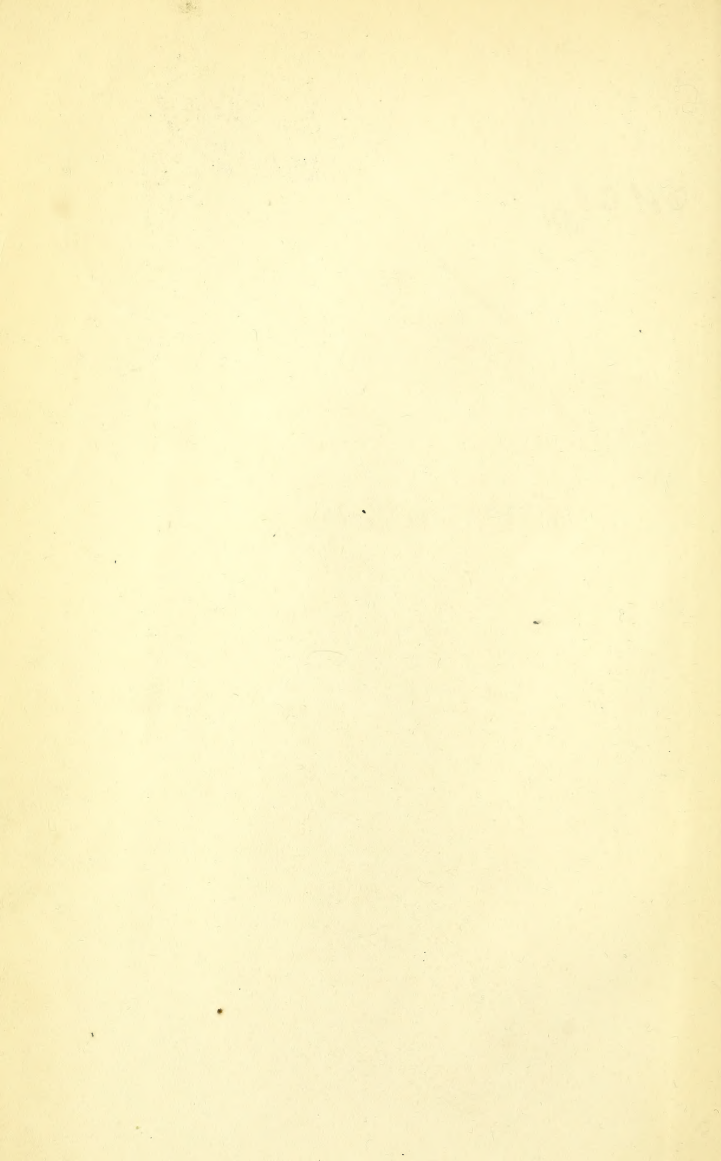






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PHYSIOLOGY.

VOL. II.

LONDON
PRINTED BY SPOTTISWOODE AND CO.
NEW-STREET SQUARE



OUTLINES
OF
PHYSIOLOGY

HUMAN AND COMPARATIVE.

BY

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ILLUSTRATED BY NUMEROUS WOODCUTS.

IN TWO VOLUMES.

VOL. II.

LONDON:
LONGMANS, GREEN, AND CO.
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SPECIAL PHYSIOLOGY.

SPECIAL PHYSIOLOGY.

THE VEGETATIVE FUNCTIONS.

THE functions to be considered under this head, are the *nutritive* and *reproductive* functions. The former include digestion, absorption, chylification, circulation, nutrition, reparation, sanguification, secretion, excretion, and respiration, together with the production of animal heat, muscular force, light, and electricity.

DIGESTION.

Amongst other phenomena produced by the waste of the solid constituents of the body, and the loss of the fluid, or watery, part of the tissues, are the special sensations of hunger and thirst, which have their seat, like other sensations, in the nervous system, and the phenomena of which have been already explained (vol. i. p. 443). These sensations of appetite, excite the desire to take food; and by the process of digestion, the food, thus taken, is prepared for absorption, and conversion into blood. The term *food* includes all substances, received into the alimentary canal, and used for the support of life, either by supplying the waste constantly occurring in the living animal tissues, or by affording materials for the maintenance of the temperature of the body. Food, therefore, contains substances which have a certain chemical relation to the tissues which it supports. These tissues, besides containing water and saline substances, are composed of proximate organic principles, having a highly complex chemical constitution (vol. i. pp. 96 to 99). Food also consists, more or less, of substances having already the same, or a similar, chemical composition: for the animal body, so far as is known, has no power of forming such proximate organic compounds out of

their component elements, or from the simpler combinations of these.

Animals, indeed, are either carnivorous or herbivorous. The carnivorous, or flesh-devouring species, obviously live upon food possessing the same chemical composition as the fluids and tissues of their own bodies; and as regards the herbivorous, or vegetable-feeding animals, their food also contains proximate principles, closely resembling those which exist in the animal body. Whatever the nature or source of the food of Animals, its proximate principles are, therefore, chemically similar; and it is to the Vegetable Kingdom, that we must attribute the power of chemically combining, under the agency of solar light and heat, the elements derived from the simpler combinations of inorganic nature, into those complex organic proximate principles which, thus elaborated in the living tissues of vegetables, constitute the nutriment of Animals. Hence, the Vegetable Kingdom derives its nourishment from, and depends upon, the Mineral Kingdom; the Animal Kingdom derives its nourishment from, and depends upon, the Vegetable Kingdom; whilst the decaying portions of the Vegetable Kingdom which are unconsumed by animals, and the particles of the bodies of animals which undergo change during life, or decomposition after death, revert to the simpler chemical compounds of inorganic nature, which, again, under the influence of the vito-chemical forces of the plant, are reintroduced into the stream of organic existence.

Sources, Varieties, and Nature of Human Food.

The food of Man may be either *solid* or *fluid*. If solid, it may be *hard*, so as to require to be broken by mastication, or *soft*, so as merely to need subdivision, before it is swallowed. Again, food may be derived from the *inorganic* or from the *organic* world; or it may be classified according to its source, whether this be *mineral*, *vegetable*, or *animal*. Thus, the alkaline and earthy salts, the traces of iron, sulphur, and phosphorus, and the large quantity of water, are derived from the *mineral* kingdom. *Vegetable* food includes the roots, stems, leaves, fruits, and seeds of plants; also certain products of vinous decomposition, as the various alcoholic beverages, and lastly, condiments, vegetable acids, and vinegar or the product of the acetous fermentation. *Animal* food consists of all the digestible parts of animals, in which is comprised

nearly every tissue, with the exception of the horny textures and the hair, even the bones yielding nutriment on being boiled. Besides this, eggs and roe, milk, butter, butter-milk, curd, cheese, and whey, are comprehended in this category.

The *chemical constitution* of food, however, is the point to which the greatest significance is to be attached; and the most useful classifications are founded on a consideration of the different nutrient proximate chemical principles which it contains. Thus regarded, the multitudinous articles of diet consumed by man, under his extremely varied conditions of life, dependent on climate, social condition, national custom, or individual habit, consist of a comparatively small number of proximate chemical constituents. The importance of these chemical distinctions of the food, was clearly indicated by Prout, and has been since established by the researches of Liebig, and many other chemists. Prout divided all nutrient substances into *albuminous* bodies, such as the albumen, fibrin, and casein of animals, and the gluten and legumin of plants; *oleaginous* substances, including the animal and vegetable fats and oils; and *saccharine* matters, comprising the various kinds of sugar. According to him, the typical form of animal food, is that supplied, by nature, to the young of mammiferous animals and man, viz. *milk*, in which fluid, casein represents the albuminous kind of nutritive substances; butter, the oleaginous kind; and sugar of milk, the saccharine kind. Besides these, milk also supplies water, and the mineral matters essential to the formation of the tissues.

A more exhaustive classification of the nutritive substances contained in food, is that which follows:—

1. *Albuminoid* substances. From the animal kingdom, *albumen*, whether derived from the white of eggs, from blood, or from the muscular or nervous tissues; *syntonin*, or the fibrinous element of muscle, some of which is contained in the expressed juice of meat; *globulin*, *cruorin*, and *fibrin*, from the blood; *casein*, derived from milk; and the *vitellin* of the yolk of eggs. The substance of the liver, pancreas, kidneys, and other glands, is also, in great part, albuminoid, mixed, however, especially in the first organ, with fat. The brain substance is also highly nutritive, containing both albuminoid and fatty matter. In this group, must be included, not only *cruorin*, or the colouring matter of the blood, but also *myochrome*, or that of muscle, both of which have an extraordinary affinity for oxygen. From the vegetable kingdom, are obtained the albuminoid substance

gluten, sometimes called *vegetable albumen*, which is chiefly obtained from the seeds of the various kinds of corn, and other grasses; also *legumin*, which has been compared to animal casein, and exists in large quantity in the seeds of peas, beans, lentils, and other leguminous plants. Vegetable albumen likewise exists, in small quantity, in the growing or soft tissues of the various succulent edible parts of vegetables and fruit, such as the cabbage, cauliflower, turnip, apple, pear, and orange.

2. *Gelatinoid* substances. These, which are derived solely from the animal kingdom, include *jelly* of various kinds, obtained from the gelatin-yielding tissues of animals, such as isinglass, which is the dried sound, or air-bladder, of the sturgeon, the areolar and fibrous tissues, tendons, and bones; also *chondrin*, or the jelly obtained from cartilages. These several tissues, however, are not supposed to contain gelatin or chondrin, when in their raw or uncooked state. Gelatinoid substances are present in broths, jellies, and ivory bone-dust. So far as their nutrient qualities are concerned, they must be distinguished from the albuminoid substances.

3. *Oleaginous* substances. These comprehend the animal fats and oils, *stearin*, *margarin*, *palmitin*, and *olein*, the fatty matters of the bile and of the brain, and those of the yolk of eggs; and also the fatty acids of butter, the butyric, capric, and caproic. To these must be added, the vegetable oils, whether solid or fluid, such as cocoa-nut oil, olive oil, and almond oil.

4. *Amylaceous* or *starchy*, *gummy*, and *saccharine* substances. These comprehend the different varieties of *starch*, such as potato starch, arrow-root, sago, tapioca, rice, and the starchy portion of wheat and other grain. The gummy substances include, besides all the natural *gums* and mucilages of fruits and vegetables, the substance named *dextrin*, which results from the transformation of starch, *cellulose* or lignin, and also *pectin*, a constituent of succulent vegetables. The *sugars* are the common, or cane sugar, and grape sugar, derived, as such, from vegetables, or produced by the transformation of starchy or gummy substances. There are also the sugar of honey, which is an animal preparation; the glycogen, or animal starch, often present in flesh, but chiefly found in the substance of the liver; *inosite*, or sugar of muscle; and lastly, the sugar of milk, *lactose*, or *lactin*, which, though usually formed in the animal economy, can also be artificially made, by acting upon starch with certain acids, at a high temperature.

5. *Stimulating* substances. These consist of three classes:

viz. first, the various kinds of *spices* or condiments, the active properties of which depend usually upon volatile or essential oils; secondly, the parts of vegetables, whether the leaves or berries, which contain the *alkaloids*, thein, caffenin, or theobromin, which are found in tea, coffee, cocoa, and the Paraguay tea. With these should probably be associated, the substances named *extractives*, viz. *cerebric acid*, which exists in nervous substance, and also in corn, especially in Indian corn; *creatin* and *creatinin*, which are found in the juice of meat, in the brain, and in the blood, the former being converted in the system into the latter; both of these act either as stimulants, or by retarding chemical change and loss in the albuminoid tissues. The thein and allied bodies certainly stimulate the heart, muscles, and nervous system. Thirdly, there are the various *alcoholic* beverages made by the fermentation of saccharine substances, such as mead, beer, cider, wine, and the stronger alcoholic fluids or spirits distilled from various fermenting saccharine vegetable juices. These substances are probably not immediately nutritive, or able to supply the waste of material, but appear rather to act as stimuli to the nervous system, and also by preventing waste. To these may be added, the several *ethers* formed in ripe fruits, and in wines, from the action of the organic vegetable acids on alcohol. This class may also include certain *organic vegetable acids*, such as the acetic acid of vinegar, the tartaric, malic, racemic, oxalic, and citric, derived respectively, from grapes or raisins, apples, gooseberries, the esculent rhubarb, and the lemon, lime, and orange; and lastly, the lactic acid existing in sauer-kraut, and in fermented cucumbers or beans, all of which are favourite articles of diet with some nations. The prevalence of the desire for acids with the food, is remarkable. Lactic acid also exists in sour milk, which is much consumed, and in the juice of meat, together with paralactic and inosinic acids.

6. *Saline, earthy, and mineral* substances. These, which are, in certain proportions, essential articles of food, soda for the blood, potash for the muscles, and lime for the bones, consist of the chlorides of sodium and potassium, the phosphates of soda, potash, and of magnesia, perhaps the alkaline sulphates, the phosphate and carbonate of lime, and oxide of iron. Minute traces of manganese and silica are also necessary, the latter being probably combined with fluorine. Such substances as alumina and copper, are probably adventitious ingredients, and of no essential importance as food.

7. *Water* is the most abundant constituent of the animal body, and is a most essential article of food. From the many offices which it performs, dissolving the food, rendering it capable of absorption and entrance into the circulation, facilitating all nutritive, secretive, and excretive processes, and lastly, maintaining the due elasticity and flexibility of the tissues, and their susceptibility of vito-chemical changes, water may be regarded as a common vehicle, in which all other articles of diet are conveyed into, through, and from the animal economy.

The albuminoid and gelatinoid nutrient substances, resemble each other very closely in composition; in addition to carbon, hydrogen, oxygen, and sulphur, they contain nitrogen, and have therefore been named, *nitrogenous* or *azotised* food; and, as these substances are especially concerned in the formation of the albuminoid and gelatin-yielding tissues of the body, which indeed cannot be built up without them, they have been designated *nutritive* or *plastic* food. Moreover, as they supply the waste which takes place in the muscular and other tissues, they have been likewise called *flesh-forming*, *tissue-forming*, or *histo-genetic*, food. On the other hand, the oleaginous and saccharine substances are composed of carbon, hydrogen, and oxygen only, and are therefore named *non-nitrogenous* or *non-azotised* food. The starchy, saccharine, and allied compounds, form the carbohydrates; whilst the fatty substances, still richer in carbon, are named hydrocarbons. As neither of these is ever supposed to be convertible, by the addition of nitrogen, into nitrogenous, plastic, or flesh-forming food, but rather, owing to their richness in carbon and hydrogen, and their poverty in oxygen, to be ultimately used for the purposes of maintaining the animal heat, either being first stored up in the body as fat, or being at once oxygenated through the respiratory process, they have been classed together under the appellation of *respiratory*, *calorific*, or *heat-forming*, food.

These distinctions, which have been chiefly explained and advocated by Liebig, undoubtedly represent a general truth; but they must be accepted with certain qualifications. In the first place, albuminoid substances may, it would seem, undergo metamorphosis, in the living body, into fatty or even starch-like substances, and so may nourish non-nitrogenous, as well as fleshy or nitrogenous, tissues. Moreover, the nitrogenous tissues of the living body, especially those of the muscles and

brain, themselves undergo a most active waste, *i.e.* a chemical decomposition, of which the essential feature is oxidation; so that, to a certain extent, they too, in being decomposed, must contribute to the evolution of heat, subserve the respiratory process, and so far act as respiratory food.

Again, chemical analysis shows, that in the brain especially, but also in muscular tissue, fatty matter is an important constituent, essential, indeed, to the composition of those tissues; moreover, starchy and saccharine matters exist in certain organs, and are convertible, in the living economy, into fat; hence the non-nitrogenous, oleaginous, and saccharine substances must, also, be regarded as nutritive or plastic food. Even in young growing animal cells, fatty matter appears to be an essential element. Again, as regards gelatin, and the gelatin-yielding tissues, which, though they contain nitrogen, have a lower chemical constitution than the albuminoid substances, it is not certain that they are convertible into, or capable of being made use of as, nutriment for the living tissues. It is now generally denied that they can be so converted into, or assimilated by, tissues which, like muscle and nerve, contain syntonin and albumen; it is even doubted whether they can be directly assimilated as nutriment, even by the living gelatin-yielding tissues themselves, which, of course, have an identical chemical composition. Such substances may, therefore, possess very limited or no nutritive or plastic qualities; and may merely be oxidised in the system, like the non-nitrogenous, respiratory food. The precise destination of the several elements of food is, however, not completely understood; but neither of the two kinds of food, the nitrogenous, or the non-nitrogenous, is alone adequate to support animal or human life; for perfect nutrition, the two must be taken together in certain proportions.

The chemical composition of most of the nitrogenous and non-nitrogenous proximate constituents of animal substances used as food, is given in the tables at pages 96 and 98, vol. i. The closely similar composition of the nitrogenous and non-nitrogenous proximate constituents of vegetable substances used as food, is illustrated in the annexed table (p. 8).

Prehension and Preparation of Food.

In the lower animals, the important act of the prehension of food, is provided for, in every case, with the most admir-

Analysis of Vegetable Proximate Constituents.

	Carbon	Hydrogen	Nitrogen	Oxygen	Sulphur and Phosph.
Vegetable Albumen . . . =	55.01	7.23	15.92	21.84	{ included with the oxygen
Vegetable Fibrin or Gluten . =	54.6	7.2	15.81	22.29	
Legumin, a similar compo- sition, but not well deter- mined }					
Thein, Caffein ($C_8H_{10}N_4O_2$) . =	49.4	5.2	28.9	16.5	
Theobromin ($C_7H_8N_4O_2$) . =	46.7	4.4	31.1	17.8	
Vegetable Oils, chiefly Oleic acid, and Glycerin (p. 96).					
Starch }					
Dextrin or Gum }					
Cellulose and Lignin }					
($C_6H_{10}O_5$) =	44.4	6.2		49.4	
Cane Sugar ($C_{12}H_{22}O_{11}$) . . . =	42.1	6.4		51.5	
Grape Sugar, Glucose, or Dextrose } ($C_6H_{12}O_6$) =	40.	6.7		53.3	
Alcohol (C_2H_6O) =	52.2	13.		34.8	
Ether ($C_4H_{10}O$) =	64.85	13.5		21.65	
Vegetable Acids :					
Citric ($C_6H_8O_7$) =	37.5	4.2		58.3	
Malic ($C_4H_6O_5$) =	35.8	4.4		59.8	
Tartaric ($C_4H_6O_6$) =	32.	4.		64.	
Alkaline and Earthy Salts and Water, the same as in Ani- mals; but Land Plants con- tain mostly Potash, and Marine Plants mostly Soda.					

able perfection of contrivance. In Man, however, the arm and hand are so wonderfully organised for other, and higher, purposes (vol i. p. 239), that their prehensile action, in the gathering, or preparation, of food, and its conveyance to the mouth, are, though essential, only subordinate offices of the upper limb. The lips and tongue, which, in the Mammalia, are devoted, mainly at least, to the taking of food, are in Man also so employed; but higher services are demanded of these

parts, and we are accustomed to associate their mechanism more especially with the faculty of speech. Lastly, the jaws and teeth, although, in animals, they frequently constitute the most important, and, in the case of the lower Vertebrata, the sole organs of prehension, can hardly be said to fulfil, in Man, in addition to their proper office of mastication, a prehensile office in reference to the food.

As regards the prehension of food, Man appears, indeed, almost at a mechanical disadvantage, in comparison with the animals beneath him, so far, at least, as concerns any special adaptation of the parts of the organism, employed for that purpose in animals. Nevertheless, he accomplishes this act with facility.

In the choice and selection of food, Man, guided by his intelligence, possesses enormous advantages over the lower animals. He ranges through the whole domain of the organic kingdom, and by the arts of acclimatisation, breeding, cultivation, and agriculture, has improved many species, both animal and vegetable, which, in their wild, and uncultivated condition, are much inferior as sources of food. The improvement of the cereal, or corn plants, of vegetables and fruits, and of the ox, sheep, and pig, and also the acclimatisation of many gallinaceous birds, and the more recent results of pisciculture, and of attempts to breed the oyster, afford proofs of this statement.

The use of *fire* for the preparation of food, is, like the employment of fire in general, peculiar to Man, who has, indeed, been designated a "cooking animal." The direct application of fire heat to food, develops peculiar empyreumatic flavors and odours, in the cooked substance, whether this be animal or vegetable; but the more important action of heat, whether applied directly, as in roasting or baking, or indirectly, through the agency of water, as in boiling, is to change the molar and molecular condition of the cooked substances. Thus, the albuminoid bodies are more or less coagulated; the gelatin-yielding tissues become swollen and partially gelatinised; fat-cells are ruptured, and fats are rendered more fluid; the various kinds of starch have their granules pulped, and the cellulose and lignin of vegetable tissue, are broken up, so as to liberate the contents of the cells. The general result of cooking, is to disintegrate, and separate the animal tissues into minuter portions, and to destroy the continuity of vegetable textures. Cooking, therefore, produces

both physical and chemical changes in the food, the tendency of which is to facilitate mastication, and the subsequent action of the digestive fluids, thus rendering them softer and more digestible.

Man also has discovered and employed as drinks, numerous beverages, obtained from the natural products of nearly every climate, by the spontaneous, or the induced, alcoholic fermentation of saccharine matter, whether this saccharine matter exist ready formed, as in the juice of the grape, or other fruits, or whether it be artificially generated by the transformation of starch into sugar, as happens when barley is manufactured into malt. Besides consuming the immediate products of fermentation, in the shape of wine, beer, and other fermented liquors, distillation is had recourse to by Man, in order to procure, in a more concentrated state, the spirit, or alcohol, generated in that fermentation. Man, therefore, not only employs the art of cooking, but also the chemical processes of fermentation and distillation, in the preparation of food, using this term in its widest sense. The precise destination of alcohol in the system will be hereafter discussed.

Other beverages are made by simple infusion or decoction, so as to dissolve out certain nutrient or stimulating substances, as from tea, roasted coffee, cocoa, and other vegetable products. Sugar is used in solution, in the sweetening or preservation of fruits, in cookery, and in preparing various articles of confectionery; it is a highly important and useful form of food. Common salt, being contained in the blood and tissues, is an essential article of food. Its use as a condiment, and also as a preservative, especially of animal substances employed as food, is very old and general. All animals are fond of salt. Its injurious influence on the quality of the food preserved in it, has long been recognised, the continued use of such food, in the form of salted provisions, favouring the production of scorbutus or scurvy. Salt hardens the muscular and other tissues preserved in it, by abstracting water from them; with this water, which appears in the brine, the soluble potash and magnesia salts, as well as the creatin and other extractives, are likewise abstracted from the meat, and pass into the preservative liquor, thus leaving the meat destitute of many alimentary principles essential to health. Indirectly, this may be the cause of scurvy; or that disease may partly depend on the direct action of the common salt taken in excess.

The employment of vinegar as a condiment, and the use of

vegetable acids, those universally favourite articles of diet, aid in the solution of nitrogenous food, and possibly of the lime salts, but they can scarcely be regarded as possessing positive nutrient properties. Other condiments, and spices, serve to stimulate the secretion of the digestive fluids, and excite the movements of the alimentary canal.

In the artificial preparation of food, so as to render it soluble, or more easy of solution, we assist the digestive function itself, which, in adapting nutrient substances, by a series of processes, for absorption into the tissues of the body, has, for its immediate aim, the minute *subdivision* and the *solution* of these substances.

The process of digestion, accordingly, includes certain *mechanical* and *chemical* acts. The former have for their object, to triturate and comminute the food, to mix it with fluids and with the various secretions in the alimentary canal, to move it within and onwards through the several portions of that canal, and lastly, to expel from the body the unabsorbed residue. The latter are accomplished by the aid of the various digestive fluids poured into the alimentary canal. Considered in the order in which they take place within the body, the several processes necessary to digestion, are *mastication*, or the chewing of the food, and *insalivation*, or the mixing it with saliva, which occur simultaneously in the mouth; *deglutition*, or *swallowing*, in which the food is conveyed through the pharynx and œsophagus, into the stomach; *gastric digestion*, which takes place in the stomach, by aid of the gastric juice, also called *chymification*, and sometimes, though erroneously, digestion proper, for further true digestive processes occur in the intestine; and, lastly, *intestinal digestion* itself, accomplished by aid of the bile, pancreatic juice, and intestinal juice, immediately preparatory to the proper act of absorption of the digested materials, by the lacteals, in which they appear as *chyle*. Absorption of certain constituents of the food, however, likewise occurs, more or less, through the capillaries of every part of the alimentary canal. The residue of the food, or *ingesta*, together with the unabsorbed secretions, form the *egesta*, the expulsion of which, constitutes the function of *defecation*.

The mechanical and chemical processes of digestion, require separate, and lengthened, consideration.

MECHANICAL PROCESSES OF DIGESTION.

Mastication and Insalivation.

The parts concerned in mastication, are the *teeth* and *jaws*, the *muscles* which move the lower jaw upon the upper one, the *muscles* of the *cheeks*, the *lips*, the *tongue*, and *palate*.

The *teeth* in Man, as in all Mammalia, are developed in two sets; a *first*, less numerous, and smaller *set*, known as the *milk*, *temporary*, or *deciduous teeth*, and a *second set*, larger and more numerous, called the *permanent teeth*.

The *milk teeth* are twenty in number, ten in each jaw. The five teeth, in either half of each jaw, commencing at the middle line, consist of two so-called *incisor teeth*, one *canine*, and two *molar teeth*. The formula of these teeth is thus written,—

$$\begin{array}{cccccc} \text{M 2} & \text{C 1} & \text{I 4} & \text{C 1} & \text{M 2} \\ \hline \text{M 2} & \text{C 1} & \text{I 4} & \text{C 1} & \text{M 2} \end{array}$$

When these teeth are shed, they are succeeded, at intervals, by the *permanent teeth*, which are thirty-two in number, sixteen in each jaw, eight in either half of each jaw; viz.

Fig. 84.

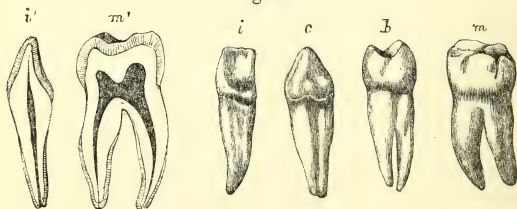


Fig. 84. Human teeth. *i*, lower lateral incisor, seen from behind. *c*, lower canine, seen from within. *b*, second upper bicuspid, seen sideways. *m*, second lower molar, seen from without. *i'*, section of an incisor tooth, showing the pulp cavity, extending from the point of the fang, the dentine, or tooth substance, the enamel on the crown, and the layer of cement on the fang. *m'*, section of a molar tooth, showing the same parts, and the pulp cavity extending into each fang. (Blake.)

commencing at the middle line, two *incisors*, one *canine*, two *bicuspids*, and three *molars*. The formula of these teeth is therefore,—

$$\begin{array}{cccccccc} \text{M 3} & \text{B 2} & \text{C 1} & \text{I 4} & \text{C 1} & \text{B 2} & \text{M 3} \\ \hline \text{M 3} & \text{B 2} & \text{C 1} & \text{I 4} & \text{C 1} & \text{B 2} & \text{M 3} \end{array}$$

Each tooth, fig. 84, *i* to *m*, consists of an exposed part, called the *crown* or *body*, and of a part buried in the gum and jaw, named the *root* or *fang*; at the junction of the crown and fang, is the slightly constricted *cervix* or *neck*. The several kinds of teeth differ in the form of their crowns, and in the number of their fangs; hence their different designations. The *incisor* teeth, *i*, have wide, thin, crowns, slightly convex in front, and smooth or marked with longitudinal furrows, but somewhat concave, or bevelled off, on their hinder surface; their edges, which, at first, present three small prominent points, are, when worn, long, narrow, and chisel-shaped, being well adapted for *cutting* purposes; hence their name. The fang is long, single, and somewhat compressed from side to side. In the temporary teeth, but much more markedly in the permanent set, the upper incisors are larger, and occupy more space transversely, than the lower ones; in the upper jaw, the middle incisors are larger than the lateral ones; in the lower jaw, the reverse is the case. The *canine* teeth, *c*, larger and thicker than the incisors, are distinguished by the pointed character of their crowns, which are very convex in front, and a little hollowed behind, and also by the great size and length of their single fang, which presents, on its sides, a slight longitudinal furrow. The upper canines, popularly called the *eye-teeth*, are larger and longer than the lower ones, and on their posterior surface, close to the gum, is found a minute tubercle. The groove on the fang, and this posterior tubercle, foreshadow the subdivided fang and double crown of the bicuspid teeth. The canine teeth are so named from their large size in the dog, though they are still larger in the great feline animals; in Man, they are more uniform in size with the neighbouring teeth, than in the larger Quadrumana and Carnivora. From their single point or *cusp*, which wears down with use, these teeth are sometimes called the *cuspidate* teeth. The *bicuspid* teeth, *b*, sometimes called *premolars*, because they are placed before the molars, and also named the *small* or *false molars*, have a double crown furnished with two pointed cusps or tubercles; viz. an outer higher, and an inner lower, one, between which is an irregular depression. The summit of the crown is quadrangular, and compressed from side to side, contrasting with the pointed canines, and chisel-shaped incisors. The fang, in the lower bicuspid, is deeply grooved on each side, but in the upper ones, is cleft for a certain distance at the point. The *molars* or *grinding* teeth, *m*, are the largest of the entire set;

the first on each side of each jaw, are the largest, and the third, or last molars, which are also named the wisdom teeth (*dentes sapientiæ*), from their late appearance, are the smallest. They have a large, nearly cuboid crown. In the upper molars, this presents four cusps or tubercles, placed at the angles of the upper surface, and separated by a crucial depression; the first and second of these teeth have the internal anterior tubercle always the largest; in the last upper molars, the two internal tubercles are blended. The crowns of the lower molars are larger than those of the upper, and are distinguished by having a fifth small cusp or tubercle placed between the outer and inner posterior cusps, rather nearer to the former than to the latter; this fifth cusp is best marked in the last lower molar tooth. The grinding surface of the lower molars is nearly square; that of the upper, rhomboidal. In the lower jaw, the two anterior molars have two fangs, but these are broad, grooved on their surface, and sometimes subdivided at their points. In the upper jaw, the fangs of the two anterior molars are three in number, two outer and one inner fang, the latter being sometimes grooved or even subdivided. The fangs of the upper molars are more divergent than those of the lower ones. In the *wisdom teeth*, or *last* molars of each jaw, the fangs are generally *connate* or united into a mass, showing marks of subdivision into two fangs in the lower teeth, and three in the upper.

The row of teeth, in each jaw, forms what is called the *dental arch*. In Man, it presents a broad, even curve, the upper dental arch being larger than the lower, so that usually it overlaps the latter when the teeth are closed, and thus saves the edges of the incisor teeth from unnecessary wear. The upper front teeth are inclined slightly forwards, and the back teeth, outwards; whilst the lower front teeth are vertical, and the lateral teeth directed somewhat inwards, an arrangement which corresponds with the greater size, and the overlapping of the upper dental arch. In Man, the entire series of teeth are characterised by being uninterrupted by any marked interval, hiatus, or *diastema*, and by their nearly even height, which however diminishes slightly from before backwards. In Mammiferous animals, the teeth are either of unequal height at different parts of the jaw, or are interrupted by larger or smaller intervals, or *diastemata*.

The *temporary* teeth, though of course, in each case, of smaller size, have forms like those of the permanent teeth of

the same name. The crowns of the incisors are chisel-shaped, those of the canines pointed, and those of the molars square, and provided with several cusps. The first upper molar, the largest of all, has three cusps, and the second four; the first lower molar four, and the second five. The fangs of the temporary incisors and canines, are single; those of the lower molars are two in number; those of the upper, three. In both jaws, they are more divergent than those of the permanent teeth.

The hard mass of a tooth is hollowed out, so as to form a cavity, called the *pulp cavity*, because, during life, it contains a soft substance named the *pulp*. This pulp cavity, fig. 84, *i'*, *m'*, varies in shape with that of the tooth; it occupies the base of the crown, and is prolonged down each fang, in the form of a small canal, which opens at the point. The pulp consists of areolar tissue, supplied with vessels and nerves, which enter at the minute opening at the point of the fang; it is the remains of the vascular and nervous papilla, upon which the tooth is originally formed.

The hard portion of the tooth surrounding the pulp, is composed of three substances; viz. the *tooth substance*, *ivory*, or *dentine*, the *enamel*, and the *crusta petrosa*, or *cement* (see fig. 84).

The dentine forms the greater part of the tooth, immediately surrounds the pulp cavity, and corresponds, in form, with the tooth itself. Its hardness is owing to the large quantity of earthy matter which it contains, its chemical composition being 72 parts of earthy to 28 of animal matter; whilst ordinary bone shows a proportion of $66\frac{1}{2}$ to $33\frac{1}{2}$. The earthy salts contain 66·7 of phosphate of lime, 3·3 of carbonate of lime, 1·8 of phosphate of magnesia and other salts, and some traces of fluoride of calcium. The animal substance is converted into gelatin on being boiled.

The dentine consists of microscopic tubes, called the *dental tubuli*, which have hard walls, and are embedded in an intermediate hard substance. These tubuli, originally described by Leeuwenhoek, commence by minute orifices on the walls of the pulp cavity, and proceed outwards in a slightly wavy course, close together; they soon divide dichotomously, and reach the superficial portion of the dentine, near the surface of which they terminate in fine branches, in loops, or in minute dilatations from which still finer branches proceed, or else in minute *dental cells*. The diameter of the inner or larger ends of the tubes, is about the $\frac{1}{4500}$ th of an inch; their

terminations are immeasurably fine. These tubuli might be compared to extremely minute Haversian canals, their finest terminal ramifications to the canaliculi, and the minute dentinal cells to the corpuscles or lacunæ of bone (vol. i. p. 47). The dentine is, indeed, regarded as modified bone. In Man, the dentinal cells are few in number, and very minute, so that their similarity to the lacunæ of bone is not so striking as it is in the teeth of the horse and other animals, in which they are larger and more numerous. In the recent state, the dental tubuli are occupied by minute processes of the tooth pulp, which serve the purposes of nutrition, and perhaps also impart sensibility to the dentine. The substance of the walls of the tubuli, is comparatively thick; its structure is not exactly known. The intermediate hard, or so-called *inter-*

Fig. 85.

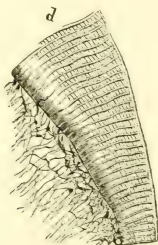


Fig. 85. Section of a portion of the crown of a tooth, magnified about 300 diameters. *d*, the enamel, composed of wavy fibres, marked with faint cross lines; the surface is bounded with a fine homogeneous layer. Beneath the enamel, is a portion of the tooth substance, showing the ends of the tubercle of the dentine, and certain irregular spaces in it. (After Kölliker.)

tubular substance, is slightly granular, and contains the greater part of the earthy matter. When this is removed by an acid, the softened animal basis is said, by some, to consist of fibres running parallel with the tubes, by others, of minute corpuscles, arranged around the tubes, and, according to another view, of fine lamellæ disposed concentrically around the pulp cavity, across the direction of the tubules, which are supposed to perforate the lamellæ.

The *enamel*, the hardest of the dental substances, and, indeed, of all known animal textures, is the dense white covering, which

protects the crowns of the teeth ; it is thickest on the edges of the incisor and canine, and on the crown of the molar teeth, and gradually becomes thinner towards the neck, where it terminates. It contains more earthy matter than any other animal tissue, viz. 96·5 per cent., of which 89·8 are phosphate of lime, with traces of fluoride of calcium, 4·4 carbonate of lime, and 1·3 phosphate of magnesia and other salts. The animal matter amounts to 3·5 per cent., the analysis showing a loss of 1 per cent. (Bibra). Berzelius estimated the animal matter at the remarkably low proportion of 2 per cent.

The enamel, fig. 85, *d*, is composed entirely of microscopic hexagonal prismatic fibres, or rods, arranged closely together upon the dentine ; they are fixed, by one extremity, to minute depressions on the surface of the dentine, and, following a somewhat wavy course, present, at their outer ends, the appearance of a hexagonal mosaic pattern, where they form the free surface of the enamel. On the crowns of the teeth, the enamel fibres are vertical ; on the sides, they become first oblique, and then horizontal. Their diameter is $\frac{1}{3500}$ th of an inch. Near the surface of the dentine, minute interstices are found between the enamel fibres, supposed to be for the purpose of nutritive permeation. In the growing tooth, by the action of an acid, the enamel may be separated into its microscopic elements, viz. into delicate prismatic nucleated cells, the walls of which coalesce, and which form moulds for the deposit of the earthy matter. In the perfectly developed tooth, the thin parietes of the cells become almost, or entirely, absorbed, and the prismatic earthy casts are blended together as the enamel fibres. On treating a growing tooth with an acid, an exceedingly delicate membrane or cuticle is found, covering the entire surface, which afterwards, becoming calcified and coherent with the ends of the subjacent fibres, forms an impenetrable protective covering to it.

The *crusta petrosa*, or *cement*, fig. 84, *i'*, *m'*, is a thin layer of true bone, which covers the fang, being thinnest next to the enamel, and thickest along the grooves and near the point ; it becomes thicker in advanced age, and sometimes fills up the minute opening leading into the pulp cavity. The *crusta petrosa* contains lacunæ and canaliculi ; the latter, in the deep layers, sometimes anastomose with the terminations of the dental tubuli ; in its thicker portions, it contains Haversian canals, surrounded by concentric lamellæ. Its outer surface is firmly attached to a fibro-vascular and sensitive

membrane, called the *periodontal membrane*, which is analogous to a periosteum, and serves to fasten the teeth in the alveoli or sockets of the jaw, being itself united to the periosteal membrane which lines the sockets.

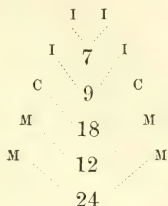
The dentine gives strength and solidity to the teeth, but being penetrated by processes of the sensitive pulp, and doubtless subject to nutritive changes, it is liable, when exposed, to suffer pain, and to undergo a process of decay resembling *caries*, which may even be repaired by an exudation of dense irregular dentinal substance. The dentine, though very hard, would not bear constant attrition; hence that singularly hard organised product, the enamel, is provided as a covering to the exposed parts of the teeth. This enamel, however, wears down, as is well seen in the incisor teeth, the primitively sharp, wavy, or notched edge of which, soon becomes worn to an even chisel-like border. The enamel often exhibits minute fissures, and in the depressions between the cusps of the molar teeth, deep cracks, which are the usual seats of commencing caries in the subjacent dentine. As life advances, the *crusta petrosa* often forms little knobs of bone upon the fangs of the teeth; and after a certain age, a deposit, partly resembling dentine and partly bone, named *osteo-dentine*, or *secondary dentine*, is sometimes slowly formed in the tooth cavity, whilst the pulp itself necessarily wastes. This deposit is produced by a conversion of the pulp, and serves to strengthen and solidify the tooth, as its crown is being worn away; in time, however, this process ends by cutting off the vascular supply of the pulp, and leads to that final stage, in which the remaining parts of the teeth drop out, and leave the edentulous jaw of old age.

The teeth of Man, and of the Mammalia generally, are not parts of the endo-skeleton, but appendages developed in the mucous membrane of the mouth, which, like the armour-plates of the armadillo, the bony scales of the crocodile, and the scales and spines of fishes, all appendages of the skin, belong to the exo-skeleton, or dermal skeleton.

The mode of development of the teeth, and the manner in which the milk teeth are shed, and the permanent teeth are cut, will be described in the section on Development. The period of the *cutting* or *eruption* of the temporary teeth is as follows:—

The milk teeth begin to appear at about the seventh month, and are completed at the expiration of the second year; but considerable difference exists in regard to the precise periods

of their eruption, frequently the first teeth appearing as early as the fifth or sixth month, and some infants being born with teeth. The annexed diagram shows the usual order and average time at which the milk teeth are cut, the numbers indicating *months*.



The lower middle incisors appear first, and generally the lower teeth are cut before the corresponding teeth of the upper jaw. Before the cutting of the teeth, the edges of the jaw, previously sharp, hard, and pale, become rounded and swollen, and of a darker colour, and the apex of the future tooth appears, like a white line or spot, through the gum.

The milk teeth, having, for a time, fulfilled the office of mastication, fall out, and are succeeded by the permanent set, destined to serve the same purpose through the remainder of life. Teeth, once formed, cannot increase in size. The milk teeth, though sufficiently large for the infantile jaws, and strong enough to resist the action of the less powerful muscles working them against the softer food consumed in the earlier periods of life, would not be strong enough for the fully developed jaws and muscles, and the harder food, of the adult. Hence, they are removed to make way for a larger set, which also, when once formed, undergo no change in size. Their formation, and calcification, commence, indeed, at very early periods of life, the ossification of the first permanent teeth beginning at the age of six months, and that of the last molars, or wisdom teeth, at about twelve years of age; yet their size is proportionate to the dimensions of the future alveoli and jaws, and to the future wants of the still undeveloped adult. The formation of the permanent teeth presents one of the clearest examples of anticipative design in the animal economy; for they are laid down, and their crowns even are fully formed, whilst the jaw itself is still too small

for their proper accommodation, and their future alveoli do not even exist.

The eruption of the permanent teeth corresponds, generally, with that of the milk set. Thus, the permanent incisors succeed to the temporary incisors, the canines of the one set, to those of the other, and the two permanent bicuspid, to the two temporary molars. The three permanent molars on each side are cut, like the milk teeth, directly through the gums.

The cutting of the milk teeth, is doubtless, in many cases, though not necessarily, a painful process; it may even produce reflex nervous irritation, which may affect the digestive, circulatory, or muscular systems, causing diarrhœa, fever, con-

Fig. 86.

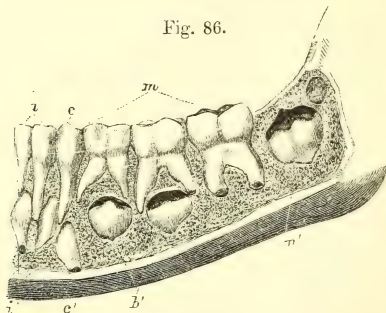
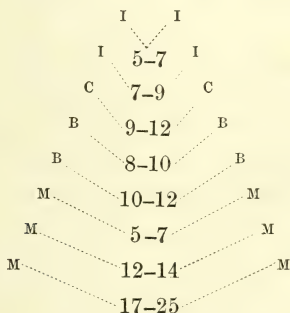


Fig. 86. Left side of lower jaw, at the age of five years, having the bony substance partly removed, to show the second set of teeth, forming beneath the temporary or milk teeth. *i*, temporary incisors. *c*, temporary canine. *m*, first and second milk molar, and first permanent molar. *i'*, permanent incisors, forming in recesses or sacs within the jaw, below the milk incisors. *c'*, permanent canine. *b'*, permanent bicuspid, commencing below the two milk molars, which they replace. *m'*, second permanent molar, rising behind the first, which is already through the gum. Above and behind this, is the sac of the wisdom tooth, or third permanent molar.

vulsions, or paralysis. Lancing the gums of children, affords relief in two ways; it removes the tension of the inflamed gums, and also leads to the formation of a yielding and easily absorbed cicatrix, in place of the firmer tissue of the gums. The cutting of the ten anterior permanent teeth, is unattended by pain, for the crown of each, passes through an opening in the gum, left by the shedding of a milk tooth; but the cutting of the permanent molar teeth, which have no precursory tem-

porary teeth, is usually a painful process, more particularly the cutting of the wisdom teeth, the jaw and gums being frequently so cramped, that the tooth has not sufficient room to rise.

At about the age of five years, immediately before the shedding of any of the milk teeth, the jaw bone contains more teeth than at any other period of life; for, besides the milk teeth, all the permanent ones, except the wisdom teeth, are found in an advanced stage of growth embedded in the bone (see fig. 86, and description). The rudiments of the wisdom teeth first appear about the sixth year. The order and date of the eruption of the permanent teeth, in the lower jaw, are expressed in *years*, in the annexed diagram; the corresponding teeth in the upper jaw appear usually, in each case, somewhat later.



In accordance with the increased number and size of the permanent teeth, contemporaneous alterations take place in both jaws. In youth, the alveolar border is almost semi-circular, but in the adult, semi-elliptical; it is, of course, shallow in the child, and deeper and broader in the adult; its hinder part especially, enlarges for the accommodation of the permanent molars. At first, the wisdom teeth of the upper jaw, lie behind and above the second molars; in the lower jaw, these teeth are embedded in the base of the coronoid processes, but descend to their proper position, as the jaw elongates. In the infant, the angle formed behind by the lower jaw, is very obtuse; in the adult, it is nearly a right angle; but in old age, when the teeth have fallen out, it again becomes more

obtuse. The obtuseness of this angle, favours the approximation of the edges of the jaws in the absence of teeth, both in infancy and old age.

The *use* of the incisor teeth is to seize and divide, like scissors, the softer portions of the food. The pointed canine teeth, stronger, and situated at the sides of the dental arches, also cut or pierce the food; whilst the bicuspid, and especially the molars, or grinders, are employed in bruising, crushing, triturating, and grinding it. The harder parts of our food are broken by the lateral, or posterior, teeth only. To accomplish these purposes, the lower jaw is made moveable upon the upper one, which has no movement, except in conjunction with the skull itself. By two projections placed at the summit of its back part, named condyles, the lower jaw articulates with the hinder part of two depressions in the temporal bones, named the *glenoid fossæ*. The condyles of the lower jaw are flattened before and behind, and widened transversely; their long diameters are, however, not quite transverse, but are inclined backwards and inwards, so that lines passing through them, would meet at a point further back in the skull. Each condyle has a loose hinge and gliding movement, in the corresponding glenoid fossa; but the two together form a firm hinge-joint, admitting also of movements, in which both condyles glide a little forwards and backwards, out of, and into, the fossæ. Moreover, when this motion is limited to one condyle, the lower jaw and teeth move sideways under the upper ones, to the right hand or to the left, the point of the chin being carried in the same direction. For the better adaptation of the articular surfaces, and the greater security of the joint, a biconcave *inter-articular cartilage*, thin or perforated at its centre, and thicker at its margins, is interposed between the condyle and the glenoid fossa, and is carried with the condyle, in all the movements of the jaw, especially in the backward and forward movements, in the lateral movements, and in extreme depression of the jaw, as in yawning. This latter motion is checked by the pterygo-maxillary ligament. Owing to the slight sliding movement of the cartilage, the axis of motion of the lower jaw is not at the joint, but a little below it, in a line with the grinding surfaces of the teeth.

The force employed in moving the lower upon the upper jaw, is muscular, and the agents immediately concerned, are the *muscles of mastication*. In opening the mouth, the lower

jaw partly descends by its own weight; but it is also drawn downwards by that portion of the digastric muscle, which ascends from the sides of the hyoid bone, and is inserted into the hinder surface of the front part of the lower jaw. The platysma myoides, a muscle of the neck, may also assist in drawing the jaw down, and so likewise do the genio-hyoid and mylo-hyoid muscles, which ascend to it from the hyoid bone, this bone being fixed by the sterno-hyoid and omohyoid muscles, which ascend to it from the sternum and the scapulæ, and also by the stylo-hyoids and the hinder portion of the digastrics, which descend to it from the styloid processes, and the inner part of the mastoid processes of the temporal bone. The external pterygoid muscles also draw the jaw forwards, and so aid in its opening.

The closure of the jaw is accomplished by muscular effort only, the muscles concerned being the most powerful of those of the head and face. The chief of these are the *temporal* muscles, which descend from the temporal fossæ at the sides of the skull; each arises from the frontal, parietal, temporal, and sphenoid bones, passes beneath the zygomatic arch, and is attached to the so-called coronoid process, at the upper and anterior end of the ascending part of the lower jaw, about an inch and a half in front of the condyle or joint. The leverage with which these muscles act, is greater than if they had been attached nearer to the condyles; their action is like that of a lever of the third order, in which strength is, to a certain extent, sacrificed to rapidity of motion. Another muscle of mastication, on each side, is the *masseter*, a very thick and powerful muscle, which descends from the lower border of the zygomatic arch and neighbouring part of the malar bone, and is inserted into the outer surface of the lower jaw, near its angle, both on its ascending and horizontal part. Each of these muscles consists of a superficial part, the fibres of which are directed downwards and backwards, and of a deep part, the fibres of which descend obliquely forwards; whilst, therefore, the whole muscle closes the jaw, the superficial part can draw this bone a little forwards, and the deeper part, slightly backwards. On the inner side of each ascending portion of the jaw, between it and the cavities of the mouth and pharynx, are two other strong muscles, named the *external* and *internal pterygoids*, which proceed from the so-called pterygoid processes of the sphenoid bones, and from the palate bones, and pass, the external one horizontally backwards and outwards,

to the inner surface of the neck of the condyle of the lower jaw, and the internal one, obliquely backwards and downwards, to the inner surface of the ascending part and angle of the jaw. The latter muscles, on each side, co-operate with the temporals and masseters, in raising the jaw, and assist a little in drawing the bone forwards; but the external pterygoids are the muscles chiefly concerned in executing this latter movement, as in protruding the chin. The backward movement is accomplished by aid of the posterior fibres of the temporal, and by the internal pterygoids. The external pterygoid of one side, causes the lateral motion of the bone upon its opposite condyle, and the lateral movement of the chin over to the other side. To accomplish the forward gliding movement of the interarticular cartilage, and, at the same time, to withdraw the two synovial membranes, situated above and below it, from the risk of pressure, certain fibres of the external pterygoid muscle are fixed to the anterior edge of the interarticular cartilage, and also to both synovial membranes. The movements of the masticatory muscles accelerate the flow of saliva and mucus into the mouth.

The chief movement, employed in dividing or lacerating soft food, is a direct ascent of the lower jaw, accomplished by the temporal, masseter, and internal pterygoid muscles. In crushing harder food, or in the bad practice of cracking nuts with the teeth, the same movement occurs, the substance being placed far back between the molar teeth, not only because these teeth are broader and stronger than the rest, but because the muscular force is used with greater effect, the nearer to the fulcrum it is exerted. The advantage of having the molar teeth in the part of the jaw nearest to the fulcrum, is obvious. A simple upward movement of the lower jaw is insufficient for the purposes of mastication; but the necessary bruising and trituration of the food, are accomplished by its backward and forward movements, and especially by the lateral movement, combined with a slight backward and forward action, which cause a rotatory or grinding motion of the lower teeth upon the upper ones.

Mastication is extremely important in the case of all solid, firm, or fibrous food, as well as of that which is hard and dry, preparing it, by comminution, for the action of the digestive fluids; when it is hurriedly or imperfectly performed, dyspepsia often ensues.

In the act of mastication, the saliva plays an important

mechanical part, as, indeed, it also does in the movements of the tongue in speech. Poured into the mouth at various points, especially from the inner side of the cheeks near the molar teeth, it not only lubricates the mucous membrane, thus facilitating the requisite and constant motion of the food in the mouth, and moistens the teeth, so as to prevent the adhesion of the food by the clogging of their grinding surfaces, but, mixed with the food, it materially assists in softening it, and converting it into a pulpy mass, fit to pass down through the membranous gullet. In mastication, the food is also mixed with a small quantity of air. It has been observed that in the mastication of dry food, such as crusts or biscuits, a larger quantity of saliva is, for a time, secreted than in the case of softer food; this is probably, in part at least, due to the more vigorous action of the muscles of mastication, exciting a general determination of vascular and nervous energy to the parts. It was found by Bernard, in experiments made by opening the œsophagus of a horse, that the mass of food swallowed, was usually mixed with about ten times its weight of saliva; when the Whartonian ducts were tied, mastication was performed much more slowly, and the food mass, taken from the œsophagus, was drier, though covered with mucus, and weighed only three and a half times its original weight.

Certain movements, which co-operate in mastication, are performed, within the dental arches, by the tongue, and on the outer side of these arches, by the *buccinators*, or *cheek muscles*, which compress the cheeks. These movements serve to place, and hold, the food between the teeth, to turn it, so that fresh portions may be subjected to the pressure of the teeth, and, finally, when it is fully masticated, to push or withdraw it from between the teeth, so that it may be swallowed. The tongue also aids in crushing soft masses of food, and forming them into suitable boluses to pass into the pharynx and gullet.

The *tongue* is a muscular organ, composed of two symmetrical halves, separated from each other by a median fibrous septum, and covered by mucous membrane and a submucous fibrous stratum. The muscles of this organ are *extrinsic* and *intrinsic*. The *former* pass into the tongue, at its base and under surface, and connect it with neighbouring parts; they are four in number in each half of the tongue, viz. the *hyo-glossus*, the *genio-hyo-glossus*, the *stylo-glossus*, and the *palato-glossus*, so named from their respective bony attachments. A few fibres of the superior constrictor muscle of the pharynx, are

also connected with the side of the tongue. The *intrinsic*, or proper muscles of the tongue, are the *superior longitudinal*, the *inferior longitudinal* or *lingualis*, and the *transverse*.

The *hyo-glossus* is a thin quadrilateral muscle, which, arising from the hyoid bone, passes upwards to the side of the tongue, to be inserted between the stylo-glossus and the lingualis. Beneath the hyo-glossus, is a flat triangular muscle, the *genio-hyo-glossus*, the apex of which arises from the inner surface of the anterior portion of the lower jaw, its base being inserted into the hyoid bone, a small portion of the pharynx, and the entire length of the under surface of the tongue. The *stylo-glossus* arises from the styloid process of the temporal bone, and divides into two portions on the side of the tongue, one, longitudinal, blending with the lingualis, the other, oblique, decussating with the hyo-glossus. The *palato-glossus*, which, as previously mentioned, forms, on each side, the anterior pillar of the soft palate, passes from the soft palate to the side and upper surface of the tongue, where it joins the fibres of the stylo-glossus.

Of the intrinsic muscles, the *superior longitudinal* muscle occupies the upper surface of the tongue, close beneath the mucous membrane, extending from its apex to the hyoid bone; some of the fibres are longitudinal, others oblique; many of them are branched or undergo subdivision, and are connected, at intervals, with the submucous and glandular structures. The *inferior longitudinal*, or *lingualis*, muscle reaches from the apex to the base of the tongue, lying between the hyo-glossus and the genio-hyo glossus, blending anteriorly with the fibres of the stylo-glossus. Between the superior longitudinal and the lingualis, are placed the transverse fibres; internally, these are connected with the median fibrous septum, and, passing outwards, they are inserted into the dorsum and margins of the tongue, where they intersect the other muscular fibres. These transverse fibres form the greater portion of the substance of the organ; they are intermixed with a considerable quantity of fat.

From the varied course of its component fibres, the tongue possesses the power of movement in all directions.

For the act of sucking, the tongue is especially important. The lips of the infant being closely applied to the breast, the tongue is drawn back, and the threatened vacuum in the mouth is filled with milk, forced in by the atmospheric pressure on the breast, as well as by the elasticity of the

distended ducts of that organ. By means of the palate, uvula, and posterior pillars of the fauces, the respiratory passages through the nose and pharynx are shut off, so that air cannot enter the mouth by that path, and, moreover, respiration is not hindered, until the act of swallowing takes place. Drinking, with the lips closed on the rim of any vessel, involves a similar mechanism; but the fluid is often allowed to enter the mouth by its gravity only. In sipping, the fluid is drawn in by an inspiratory movement; and, most commonly, the act of drinking is performed partly by sipping, and partly by pouring the fluid into the mouth. In drinking from a stream, the lips are protruded and submerged, and a combination of sucking with oral inspiration, takes place.

Deglutition.

Deglutition, or the act of *swallowing*, is that mechanical process, by which the food is passed from the mouth, through the opening called the *fauces*, into the *pharynx*, and thence along the *gullet*, into the stomach. This act is usually described as consisting of three stages:—first, that in which the food is forced backwards from the mouth, through the fauces, into the pharynx; secondly, that in which it is made to traverse the middle and lower part of the pharynx to the gullet; and thirdly, that in which it descends along the gullet, and enters the stomach.

The *first stage* of deglutition is performed by aid of the *tongue*, the hinder part of the *hard palate* and the *soft palate*, together with the so called *pillars of the fauces*. The hard palate is formed by parts of the superior maxillary and palate bones, covered by periosteum and a dense mucous membrane. The soft palate descends, like an apron, from the posterior border of the hard palate, and forms the upper margin and sides of the opening, seen on looking into the mouth, called the fauces. The arched border of this opening, forming the *isthmus of the fauces*, presents, in the middle line above, the pendulous body, named the *uvula*. Two prominent ridges on each side, are called the *pillars of the fauces*; the *anterior pillars* pass down on the sides of the tongue, the *posterior pillars*, on the sides of the pharynx; between the two pillars, on each side, is a depression, in which are lodged the soft, projecting, oval, or almond-shaped, somewhat rugose, glandular bodies, named the *amygdalæ* (almonds), or *tonsils*. These

bodies present a number of follicular depressions, the sides of which are surrounded by small closed spherical sacs, analogous to those of the so-called Peyer's patches in the intestines; they have thickish walls, lined by an epithelium, and contain a tenacious greyish white secretion; sometimes they open on the surface.

The mucous membrane of the under surface of the soft palate, is covered with a squamous epithelium, and possesses numerous compound racemose mucous glands. The mucous membrane of the upper surface, turned towards the superior part of the pharynx, is continuous with that of the nasal fossæ, and, near the openings of the Eustachian tubes, has a ciliated columnar epithelium. Between the two layers of mucous membrane, which join at the free border of the soft palate, are found, besides areolar tissue, bloodvessels, lymphatics, and nerves, a number of symmetrical muscles, by means of which, the soft, pendent, valve-like palate, is rapidly moved in various directions. Thus, the palate and uvula are raised by the *levator palati*, a thin sheet of muscular substance, which descends from the petrous part of the temporal bone and from the Eustachian tube, to the back of the soft palate; moreover, two small auxiliary muscles descend within the uvula, constituting together the so-called *azygos uvulæ* muscle, which elevates the uvula. Descending from the pterygoid processes of the sphenoid bone, and from the Eustachian tube, on each side, is a muscle, terminating below, in a little tendon, which turns beneath the *hamular*, or hooked-like end of the pterygoid process, and so, changing its direction, spreads out towards the middle line within the soft palate, and unites with its fellow of the opposite side. This muscle, acting from its point of reflexion over the hamular process, tightens and spreads out the soft palate, hence its name, *circumflexus*, or *tensor palati*. The two pillars of the fauces, on each side, likewise contain small muscles; those within the anterior pillars, are named, from descending to the tongue, the *palato-glossi* muscles; and those within the posterior pillars, from passing to the sides of the pharynx, the *palato-pharyngei* muscles. These muscles draw the soft palate downwards, and either backwards or forwards, in the direction of the tongue or palate; by their joint action on the two sides, they also contract the aperture of the fauces to a triangular fissure, which can then be completely closed by the uvula. By the variously combined actions of the surrounding muscles, the fauces can

be closed, whether the palate be drawn upwards or downwards. By the approximation of the posterior pillars to the uvula, and by the simultaneous elevation of the palate, the middle part of the pharynx can be shut off from its upper part, so that this latter, or the respiratory, portion, which communicates with the nasal fossæ, is separated from the middle part, through which the food has to descend.

In the first stage of deglutition, the lower jaw is raised, the mouth is closed, and its cavity made smaller; the mass of food, sufficiently masticated, and softened by the saliva, is placed between the tongue and the hard palate, and is then pressed backwards, by a movement of the tongue, beneath the slightly sloping soft palate, which is rendered tense by the circumflex muscles. The anterior pillars of the fauces are separated, to receive the mass, whilst the posterior pillars and the uvula, by being elevated and approximated in the manner just described, shut off the upper part of the pharynx and the posterior nasal openings. The tongue, becoming shorter and thicker, its posterior part is rendered convex, and, by means of the mylohyoid muscles, which form the muscular floor of the mouth, and also by the digastrics, stylohyoids, and thyrohyoids, is then forced upwards and backwards, and following the mass of food, propels it, through the fauces, into the middle portion of the pharynx; thus is completed the first stage in the act of deglutition.

The *second stage* of deglutition is performed through, and by, the *pharynx*. This is a musculo-membranous sac, or bag, about $4\frac{1}{2}$ inches in length, and wider above than below, which is suspended from the base of the skull, in front of the vertebral column, and behind the cavities of the nose, mouth, and larynx, with all of which it communicates. It is through the larynx, that the air passes to and from the lungs. On a level with the lower border of the larynx, the pharynx becomes continuous with the œsophagus, or gullet. The pharynx, fig. 87, has seven openings leading into it. At its upper part in front, are the two posterior nares, *n*, or nasal openings; at each side, are the apertures of the Eustachian tubes, which lead to the tympanic cavities of the ears; these four openings are above the level of the soft palate. Below the soft palate, *p*, the pharynx opens, by the isthmus of the fauces, into the mouth; lower down, beyond the root of the tongue, is the opening, *e*, into the larynx, *l*; at its termination, is that leading into the œsophagus, *o*. The walls of the pharynx consist chiefly of three pairs of, so-called *constrictor*, muscles,

supported by areolar tissue, and lined throughout by a mucous membrane, continuous with that of the nasal cavities, Eustachian tubes, mouth, larynx, and gullet. The constrictor muscles, named, from their relative positions, superior, middle, and inferior, overlap each other from below, that is, in the opposite direction to the slates of a roof, the inferior muscle being external to the middle one, and the middle one external to the upper one; the superior muscle, which is open in front,

Fig. 87.

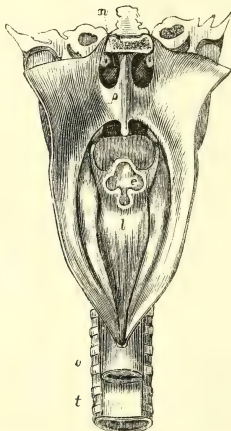


Fig. 87. Back view of the pharynx and part of the oesophagus, suspended from the base of the skull, and laid open behind. *n*, openings of the nasal cavities, called the posterior nares, separated by a median septum. *p*, soft palate, with the uvula depending from it, in the centre. Below this, the arches of the fauces, bounded by its posterior pillars: beneath this arch, is seen the back of the tongue. *e*, the epiglottis, or valve which protects the superior aperture of the larynx. *l*, the back of the larynx, seen in the opened part of the oesophagus. *o*, the oesophagus. *t*, the trachea, or windpipe.

is, therefore, embraced, at its lower end, by the middle muscle, whilst this again is embraced by the inferior constrictor. Considered together, these constrictor muscles are attached, above, to the base of the skull; in front and at the sides, to various parts of the bones of the skull and face, and also to a fibrous band passing from the styloid process of the temporal bone to the lower jaw; still lower down, to the side of the

tongue, to the stylohyoid ligament, and the hyoid bone; and, lastly, to the thyroid and cricoid cartilages of the larynx. Posteriorly, the fibres of the constrictor muscles, sweeping backwards in a curved direction, meet at a raphé, or median line, along the back of the pharynx. Spreading out on each side of the pharynx, is the stylo-pharyngeus muscle, which descends from the styloid process, and also the *palato-pharyngeus*, which passes down in the posterior pillar of the fauces. The upper portion of the pharynx, above the level of the soft palate, is exclusively respiratory, and its mucous membrane is covered with a columnar ciliated epithelium; the middle portion, through which not only air, but food and drink pass, and the lower portion below the laryngeal aperture, which is devoted exclusively to the passage of food and drink, are covered with a squamous non-ciliated epithelium. Numerous simple and compound racemose mucous glands open upon the pharyngeal mucous membrane, and moisten it with their secretion.

In the *second stage* of deglutition, the softened mass of food, forced, by the backward movement of the tongue, into the middle portion of the pharynx, is compressed, in rapid succession, from above downwards, by the lower fibres of the superior constrictors, and more especially by those of the middle and inferior constrictors, and thus is propelled *rapidly* into the upper end of the gullet. At the same time, the upper fibres of the superior constrictors, and especially the fibres of the stylo-pharyngei muscles, draw upwards, and somewhat outwards, the pharyngeal walls over the mass of food, as this is forced downwards. The super-position of the constrictors, one upon the other, from above downwards, facilitates the propulsion of the food in that direction; moreover, the food itself meets with no obstruction from the edges of the two lower constrictors, as would have been the case, had the imbrication of the muscles been in the opposite direction. The second stage of deglutition is rapidly performed, because respiration is suspended during its occurrence. Provision must also be made, during this stage of deglutition, for the safe transit of drink and food through the pharynx into the gullet, without any drop or particle being forced upwards into the nasal fossæ, where it would excite irritation, or downwards into the larynx, whence it would descend into the windpipe, and cause coughing, difficulty of breathing, or suffocation. The posterior nares are accordingly protected by the elevation

and tension of the soft palate above the middle portion of the pharynx, in the mode already described (p. 29), so as to form an inclined plane, beneath which the food glides into the pharynx, as this ascends to receive it. At the same time, the opening into the larynx is protected by the epiglottis, a leaf-like valve, situated at the root of the tongue (vol. i. p. 250), fig. 87, *e*, fig. 9, *e*. This valve, in the ordinary condition of the parts, stands erect, with its free margin directed upwards; the larynx then communicates with the middle portion of the pharynx, and air can pass from the nose, and mouth, if that be open, to and from the windpipe and lungs. When, however, the tongue is raised, and pressed backwards at the end of the first stage of deglutition, the larynx is elevated, and the mass of food, or the portion of liquid, then swallowed, presses the previously erect epiglottis downwards and backwards, so as, together with certain folds of the mucous membrane connected with its borders, completely to close the opening into the larynx, whilst the food or drink is passing by it, into the lower portion of the pharynx. The moment the solid or fluid has thus passed down, the tongue resumes its previous position, the epiglottis is again erected by the elastic folds connecting it with the anterior part of the larynx and root of the tongue, and the air passage is once more free for the purposes of respiration.

The *third stage* of deglutition is performed by aid of the muscular walls of the *gullet* or *œsophagus*. This musculo-membranous tube is that portion of the alimentary canal, which extends from the pharynx down to the stomach. It measures about nine inches in length, and is the narrowest part of the alimentary canal, being itself narrowed at its lower, but narrowest at its upper end. It descends through the lower part of the neck and through the whole length of the thorax, and then, perforating the diaphragm, opposite the ninth dorsal vertebra, enters the abdominal cavity, and immediately opens into the stomach. It is supported upon the vertebral column, being placed between the carotid arteries, and behind the trachea, the heart, and the arch of the aorta; below the latter, it lies in the space between the two pleuræ, to the right, and then in front, of the descending aorta; it traverses the diaphragm through a special opening, named the *œsophageal* opening. The walls of the *œsophagus* are composed of three coats, muscular, areolar, and mucous.

The *muscular* coat consists of an external layer of *longitudinal*

fibres, and an internal layer of *circular fibres*; at the upper end of the œsophagus, these fibres are chiefly striated, and striated fibres are to be found in smaller numbers even down to its lower end; but the great mass of the muscular coat consists of the plain, or unstriped, muscular fibres. The areolar coat is a soft distensible tunic, which supports the mucous coat. The mucous coat, reddish above, and pale below, is thick, and when the œsophagus is closed, it is thrown into numerous longitudinal plicæ; in this state, a section across the tube presents no cavity, but, in its centre, a radiating or branching cleft, formed by the meeting of the plicated folds. The pharynx is permanently open, as far as the aperture leading into the larynx, but its lower portion, and the whole length of the œsophagus, are habitually closed, their sides being always in contact, excepting when solids, fluids, or gases are passing through them; they are examples of what are called *potential cavities*. When, however, any solid or fluid is passing down the œsophagus, the longitudinal plicæ of its mucous coat are obliterated. This membrane is beset with papillæ, and covered with a many-layered squamous epithelium, which, at the lower end of the œsophagus, at the line of junction with the stomach, abruptly changes its character, and presents a crenulated border. The mucous membrane of the œsophagus is provided, especially at its upper and lower ends, with small compound mucous glands.

In the third and final stage of deglutition, the food, pressed down by the muscles of the pharynx, first distends the walls of the œsophagus, the muscular coat of which, however, speedily contracts above the morsel, and so urges it further downwards; the part thus dilated, then contracts above the mass of food, which is thus driven on, and so, by a succession of similar acts, is propelled, in separate portions, into the stomach. This successive contraction of the muscular coat of the œsophagus, from above downwards, is called *vermicular* or *peristaltic*. The circular fibres contract, in a wave-like manner, from above downwards, and are the propulsive agents; whilst the longitudinal fibres, drawing up and widening the walls of the œsophagus, over the sides of the morsel of food, facilitate its descent. Gravitation, though it may assist, has but little influence on, the downward movement of food or liquids. The resistance to be overcome, is slight, consisting only of the elastic pressure of the walls of the œsophagus and of the surrounding parts. Solid substances, and even fluids, are habitually swallowed by

the horse and other animals, against the force of gravity; and certain clowns can perform the feat of eating and even drinking, whilst "standing upon their heads." The rate of motion of food through the œsophagus, is not so rapid as that through the pharynx. Ordinarily, the movement causes only a slight sensation at the upper end of the œsophagus; but if the morsel be too large, the act is painful, especially as the mass is passing through the diaphragmatic œsophageal opening. As the œsophagus receives fibres coming from the spinal accessory nerves, but reaching it through the pneumogastrics, division of the latter in the neck, paralyses the lower part of this tube, so that the food remains in it, and distends it. It also receives sympathetic nerve fibres.

The three stages of deglutition are distinguished from each other in a remarkable manner, according to the mode in which they are regulated, or governed, through the nervous system. The *first* stage is *voluntary*; we place the food between the tongue and the palate, and, by an effort of the will, pass it backwards through the fauces, into the pharynx. Even the accompanying movement of the soft palate, to shut off the nasal fossæ, which is an associated movement, so determined by habit as to be unconsciously performed, is nevertheless a voluntary movement, or at least one which, by trifling practice, may be voluntarily performed. The *second* stage is, however, wholly *involuntary* and *automatic*, and is performed through the intervention of a reflex action, though it may be partly imitated by the will. No sooner has the food reached a certain part of the fauces, than it excites afferent nerves distributed to that part, the impressions on the fibres of which, being conveyed to a certain nervous centre, are reflected, through efferent fibres of other nerves, to the various and numerous muscles required to contract; and, by the simultaneous action of these, this stage of deglutition is rapidly performed. Whilst, then, the first stage, which involves no obstacle to respiration through the nose and pharynx, is voluntary and deliberate, the second stage, during which respiration must be suspended, is involuntary and rapid, and, moreover, is not entrusted to movements requiring practice, habit, or attention, to ensure their perfect co-operation, but is performed as promptly, efficiently, and safely, the first time by the new-born infant, as at any after period of life. The accidental passage of food or drink into the air-passages, with its accompanying inconveniences, incidentally proves the advantage of

the perfect performance of this movement. The afferent nerves concerned in this important reflex act, are those supplying the mucous membrane of the fauces and neighbouring parts of the pharynx, viz. the palatal branches of the fifth pair, and, chiefly, the pharyngeal branches of the glosso-pharyngeal and pneumo-gastric nerves; the efferent or motor fibres are contained, some in the former, but mostly in the latter nerves, being, however, derived partly from the spinal accessory nerves (vol. i. p. 336). Some also belong to the hypoglossal, which governs the movements of the tongue, and certain muscles of the neck; to the facial nerve, which supplies the digastric and stylohyoid muscles; and perhaps a few to the cervical spinal nerves. The reflex nervous centre is situated in the medulla oblongata, and upper part of the spinal cord. The *third* stage of deglutition is also entirely *involuntary*, and chiefly, if not wholly, *reflex*. The afferent fibres concerned, are contained in the œsophageal branches of the pneumo-gastric nerves, and the efferent fibres are included in the same branches, derived partly, however, from the spinal accessory nerves. It is supposed by many, that the non-striated muscular fibres of the œsophagus, may be *directly* stimulated by the substances swallowed, without the intervention of any reflex nervous action.

Movements of the Stomach.

The *stomach*, figs. 13, 89, s, the dilated part of the alimentary canal, into which the œsophagus opens above, and from which the small intestine leads below, is a musculo-membranous bag, of a peculiar shape, extending across the abdominal cavity, from left to right, in front of the vertebral column, just below the diaphragm and liver, immediately behind the anterior wall of the abdomen, and above the transverse colon. It is somewhat pear-shaped, the wider end, *fundus* or *cardiac* end, fig. 89, o, being turned to the left side, and the smaller or *pyloric* end, p, which ends in the small intestine, being turned to the right side. The œsophagus enters the stomach a little to the right of the cardiac end. The upper border of the stomach is concave, and is named the *lesser curvature*; the lower border, convex, is called the *greater curvature*; the left end of the stomach, beyond the entrance of the œsophagus, is named the *great cul-de-sac*, and a slightly dilated part of the convex border, towards the left end of the stomach, is called the *lesser cul-de-sac*. After death, the human stomach sometimes has

an hour-glass form, being constricted across its middle, or somewhat nearer its pyloric end. The stomach has two apertures, one named the *œsophageal* or *cardiac* opening; and the other the *pyloric* opening. It is attached, by its œsophageal end, to the diaphragm, and, by its pyloric end, to the back of the abdomen; the lesser curvature is attached, by a double fold of the peritoneum, or lining membrane of the abdomen, to the under surface of the liver; the left end, or great cul-de-sac, of the stomach, is connected, by a similar fold, with the spleen, and the greater curvature is loosely attached, by like folds, to the transverse colon. The greater curvature is the most movable part of the organ, which, when empty, is flattened on its anterior and posterior surfaces; but, as its cavity is filled, it is tilted forwards and upwards, so that its anterior and posterior surfaces are then turned, respectively, obliquely upwards and forwards, and downwards and backwards, the œsophageal and pyloric ends remaining almost stationary. The stomach descends with the diaphragm during inspiration, and ascends in expiration; its state of distension affects the cavity of the chest, and, when over-distended, causes dyspnœa and palpitation of the heart.

The capacity of the stomach is most variable, ranging from complete emptiness, with its walls in contact with each other, to a condition of full distension, in which it may hold three pints. When moderately full, it measures 12 inches in length, by 4 in diameter. Its weight is about $4\frac{1}{2}$ ozs.

The membranous walls of the stomach consist of four coats, viz. commencing from without, the *serous*, *muscular*, *areolar*, and *mucous* coats, all of which are held together by a more or less extensible areolar tissue. The *serous* coat, thin, transparent, and smooth, is a part of the peritoneal lining of the abdomen; the anterior and posterior surfaces of the organ, are covered by distinct layers of the peritoneum, which, leaving it along its greater and lesser curvatures, become applied to each other, to form the double supporting folds named *omenta*, by which the stomach is held in connection with other parts. The serous coat is elastic, and thus accommodates itself to the variable state of distension of the organ, which is also facilitated by a loose interspace between the two peritoneal layers along its curvatures. The *muscular* coat, to which the serous coat adheres by fine areolar tissue, contains three layers of fibres, named, from their direction, longitudinal, circular, and oblique. The *longitudinal* fibres, which are next beneath the serous coat,

are continuous with the longitudinal fibres of the œsophagus; they spread out over the stomach, being accumulated in great numbers along the lesser curvature, in smaller numbers along the greater curvature, and only thinly scattered upon the anterior and posterior surfaces of the organ. At the œsophageal opening, they form the so-called *stellate* fibres, and, at the pylorus, they are again disposed in a uniform layer, and become continuous with the longitudinal fibres of the small intestine. The *circular* fibres, internal to the longitudinal ones, form thin circular fasciculi at the great cul-de-sac, and surround the whole extent of the stomach up to the pyloric end, where they are collected into a dense ring, which projects inwards, and forms an annular sphincter muscle. This projecting ring,

Fig. 88.

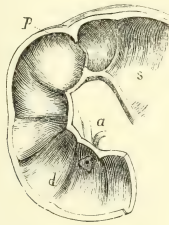


Fig. 88. Vertical section through the pyloric end of the stomach, and the curved part of the duodenum, to show the circular fold, or annular valve, at the pylorus. *s*, small part of the stomach. *d*, part of the duodenum. *p*, the pylorus, or pyloric opening of the stomach, with its annular valves. *a*, ends of the common bile duct, and the hepatic duct, entering the left side of the bend of the duodenum, to open internally by a common orifice. Much reduced in size.

covered, on its interior, by the mucous membrane, constitutes the *pylorus* or *pyloric valve* (πύλη, a gate), fig. 88, *p*, the muscular fibres of which can partially, or completely, close the pyloric aperture of the stomach. The *oblique* muscular fibres do not, like the longitudinal and circular set, to which they are internal, extend over all parts of the stomach; from around the œsophageal opening, where they are continuous with the circular fibres of the œsophagus, and form a sort of sphincter, they may be followed for a short distance on the great cul-de-sac of the stomach, spreading obliquely downwards on its anterior and posterior surfaces. The muscular

fibres of the stomach are pale, and, for the most part, non-striated, though a few, in the longitudinal layer, present traces of indistinct striæ.

The *areolar* coat of the stomach, sometimes called, from its position, the *submucous* coat, consists of dense areolar tissue, containing some fatty tissue, and a delicate layer of unstriated muscular fibres. It supports the mucous coat, and, like it, is of greater extent, and less expansible, than the muscular and serous coats; with the muscular coat, it is connected by very loose areolar tissue, so that in the empty condition of the stomach, it is thrown, together with the mucous membrane, into numerous irregular, but chiefly longitudinal, folds, called *rugæ*. The bloodvessels, lymphatics, and nerves, belonging to the mucous coat, subdivide in the areolar coat, before they enter the mucous membrane. From the number of vessels in it, the areolar tunic was formerly named the *vascular* coat, and from its white colour, the *nervous* coat; both terms, however, are objectionable. Its muscular fibres are supposed to assist, by their contraction, in the process of absorption.

The innermost, or *mucous* coat of the stomach, is a soft, pulpy, smooth, membrane, of a pale straw colour, after death, but of a pink, or bright red, hue during life, being much darker during digestion. It is habitually moistened with mucus. It adheres firmly to the areolar or submucous coat, and follows the folds or *rugæ* seen in the empty stomach, but which are completely obliterated, when this organ is distended. The mucous membrane is provided with multitudes of glands, to be hereafter described, which secrete the gastric juice. The bloodvessels and lymphatics are numerous. The nerves of the stomach are derived, partly from the large terminal branches of the pneumogastric or vagi nerves, which are joined by the splanchnic branches of the sympathetic, and partly also by the sympathetic branches, proceeding along the arteries from the cœliac or solar plexus.

The stomach is a dilated portion, or diverticulum, of the alimentary canal, intended for the reception and retention of successive portions of fluid, and of masticated and insalivated solid food, in order that whilst the watery and dissolved parts are absorbed, the solid substances may be subjected to the action of the gastric juice. Besides these purposes, for which it is fitted by the extensibility of its serous and muscular coats, and by the loose *rugæ* of its less expansible submucous and mucous

tunics, the stomach also, by aid of its muscular fibres, impresses peculiar movements upon the food in its interior, and urges onwards through the pylorus, into the small intestine, those portions which are sufficiently softened and digested by the gastric juice. In these movements, the longitudinal fibres shorten the stomach; the circular fibres lessen its diameter, acting peristaltically from its cardiac onwards to its pyloric end, whilst the oblique fibres draw the sides of the organ over the alimentary mass. When the stomach is empty, the several sets of fibres contract it in every direction, some narrowing it, and others shortening it, and so reduce it to its smallest possible dimensions. The pyloric part diminishes relatively less than the cardiac portion. When, however, the stomach contains food, its internal surface is kept in close contact with this, and the different fasciculi of each layer acting consecutively, give rise to complicated movements in certain directions. The combined result of these, is a remarkable *rotatory*, or churning, motion, which urges the food from the great cul-de-sac along the lower border of the stomach, towards the pylorus, and thence back, along the upper border to the great cul-de-sac again, and so on: such rotation is said to occupy from one to three minutes (Beaumont). In order to prevent regurgitation of the food into the œsophagus, especially during effort with the abdominal muscles, the cardiac orifice is kept closed by the circular fibres of the lower end of the œsophagus, aided by the edges of the opening in the diaphragm; the pylorus is closed by its proper muscular ring. As the outer layer of the alimentary mass becomes digested, and converted into a pulp, it is pressed, by the peristaltic action of the circular fibres, through the pylorus, and escapes at intervals, into the duodenum. As this pulpy portion is expelled, fresh layers of the food mass are brought into contact with the gastric walls; towards the end of digestion, larger quantities pass the pylorus. Whilst the pylorus permits the passage out of the stomach, of the pulpy products of gastric digestion, such solid substances as do not yield to the digestive process, are not allowed to pass, apparently because they excite the contraction of the circular pyloric muscular fibres. Such substances, as well as fish bones, buttons, plum stones, or other bodies accidentally swallowed, remain in the stomach for some time after the evacuation of its digestible contents; but after a certain delay, the pylorus relaxes, and allows them also to pass into the intestinal canal. The move-

ments of the stomach are partly reflex, being excited through the pneumogastric nerves, as is shown by experiments on animals; but it would also seem probable that a direct stimulation of its muscular fibres may co-operate. The sphincter fibres at the cardiac end, appear to be under the government of the sympathetic nerves. It is not known whether the contraction of the pylorus is a reflex act.

The gastric movements aid in the function of digestion, by rotating the food in the stomach, thus exposing all parts of the digesting mass to the action of the gastric fluid, and by continually removing the softer parts from the surface, and expelling them gradually through the pylorus, so that fresh portions of that surface are then exposed. The pressure exercised upon the contents of the stomach, may further assist in the process of venous absorption. It is to be observed, however, that portions of food, placed in perforated metal tubes or balls, and introduced into the stomach, are nevertheless digested.

Movements of the Intestines.

The *intestinal canal*, fig. 89, *d* to *r*, or portion of the alimentary canal extending from the stomach downwards, is divided into a longer and narrower part, called the *small intestine*, *d* to *i*, and a wider and shorter part, named the *large intestine*, *c* to *r*.

The *small intestine* extends from the pylorus *p*, to a valvular opening leading into the large intestine, *c*; it measures about 20 feet in length, and becomes somewhat, though slightly, narrower from above downwards. This long tube lies in *coils*, or *convolutions*, occupying the middle and lower part of the abdominal cavity, and the pelvis, fig. 13. It is supported by a broad double fold of the peritoneum, named the *mesentery*, which is attached, by a shorter posterior margin, to the back of the abdomen, but is connected by a longer anterior margin, with the back of the small intestine, so that both it and the intestine are thrown into folds, which are capable of constant change in form and position. The layers of the mesentery are prolonged over the intestine, and form its outer or serous coat; and between these two layers, are contained the bloodvessels, lymphatics and lymphatic glands, and the nerves of the intestine, all of which help to support this part.

The small intestine commences on the right side of the vertebral column, beneath the right lobe of the liver, and after

undergoing its numerous convolutions, terminates in the lower part of the right side of the abdomen. For purposes of

Fig. 89.

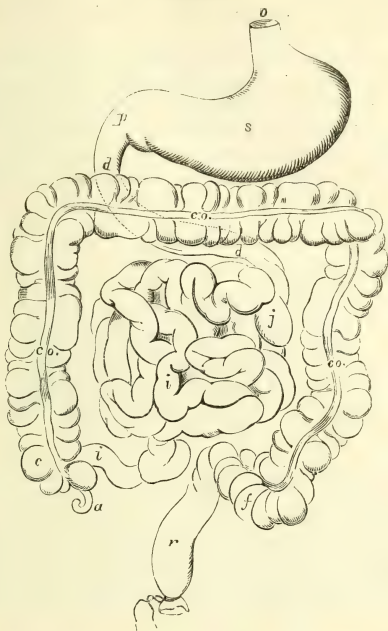


Fig. 89. Diagram, showing the abdominal portion of the alimentary canal, its subdivisions, and the general position of these in the abdomen. *s*, the stomach. *o*, the cesophageal, or cardiac end. *p*, the pylorus. *d, d*, the duodenum, or first portion of the small intestine, curving from right to left. *j, j*, coils of the jejunum, or second part of the small intestine. *i, i*, coils of the ileum, or third and last part of the small intestine. *c*, the cæcum, or first part of the large intestine, with its vermiform appendix. *co, co, co*, ascending, transverse, and descending portions of the colon. *f*, sigmoid flexure of the colon. *r*, straight intestine or rectum. The small intestine is seen to occupy the middle of the abdomen, and to be surrounded on three sides by the large intestine.

description, it is said to be composed of three portions: first, of a short portion named the *duodenum*, *d, d* (*duodeni*,

twelve), because it corresponds in length to the width of twelve fingers placed side by side ; secondly, of a longer portion named the *jejunum*, *j* (*jejunus*, fasting), from its being usually found empty after death ; and, lastly, of a still longer portion named, from its numerous coils or convolutions, the *ileum*, *i* (*εἰλεῖν*, to coil).

The *duodenum*, *d*, *d*, is about 8 or 10 inches long ; it is the widest part of the small intestine, measuring from $1\frac{1}{2}$ to $1\frac{3}{4}$ inches in diameter ; it is also the most fixed part, having no mesentery, the peritoneum merely covering it in front, except near the stomach. The duodenum describes a horse-shoe like curve, the convexity of which is turned to the right ; first it

Fig. 90.

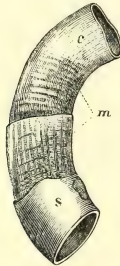


Fig. 90. Portion of the small intestine, dissected, to show the position of its several coats. *s*, the outer, smooth, serous or peritoneal coat. *m*, the muscular coat, composed of an outer layer of longitudinal fibres, and an inner layer of circular fibres. *c*, the submucous and mucous coats united together. Much reduced in size.

ascends, for about 2 inches, towards the under surface of the liver and gall-bladder ; then, it descends in front of the right kidney ; next it passes from right to left, across the second lumbar vertebra, the attachment of the diaphragm, the ascending vena cava, and the aorta, and passing slightly upwards, joins the jejunum, opposite a line corresponding with the superior mesenteric artery and vein. In the concavity of the curve of the duodenum, is placed the right end or head of the pancreas, which is here attached to the intestine. The common bile duct and the pancreatic duct, open into the duodenum.

The *jejunum*, *j*, forms about two-fifths, and the *ileum*, *i*, *i*,

the remaining three-fifths of the part of the small intestine below the duodenem. The jejunum occupies the middle and left regions of the abdomen; whilst the ileum is placed in the middle, lower, and right regions, and, occasionally, partly descends into the pelvis. The termination of the ileum in the large intestine, *c*, is situated in the right iliac fossa. The jejunum has thicker and dark coloured coats, and is somewhat wider than the ileum, the average diameter of the former being $1\frac{1}{4}$ inch, that of the latter 1 inch.

The membranous walls of the small intestine are composed, like those of the stomach, of four coats; viz. the serous, muscular, areolar, and mucous coats. The *serous* coat, fig. 90,

Fig. 91.

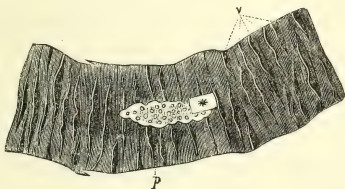


Fig. 91. Portion of the small intestine, laid open to show the smooth internal coat or mucous membrane, which is here thrown into numerous transverse double folds or ridges, which are permanent. These are the valvulæ conniventes, *v*. A patch of the so-called Peyer's glands, or glandulæ agminatæ, or aggregatæ, with its little component round sacs, is shown at *p*. The oblong white piece of card, partly covering the patch of Peyer, and marked with an asterisk, *, shows the relative size of the piece of mucous membrane represented in Fig. 98.

s, derived from the peritoneum, is thin and elastic, to permit of various degrees of distension; whilst the smoothness and moisture of its free surface, facilitate the changes of form and position of the intestinal convolutions upon each other, and upon adjacent parts. The *muscular* coat, *m*, consists, as elsewhere, of an external layer of longitudinal, and an internal layer of circular fibres. The longitudinal layer is thinner than the circular layer, and is most distinct along the free border of the intestine; the circular fibres are arranged more closely together. The *areolar* or *submucous* coat, *c*, is loosely connected with the muscular coat, but more firmly with the mucous membrane, which it supports. Thin crescentic

extensions of this areolar coat project transversely, at intervals, into the interior of nearly every part of the small intestine, and, covered, on both sides and at their edges, by the closely adherent mucous membrane, constitute the so-called *valvulae conniventes*, fig. 91, v. These valves may be displayed by opening the intestine, and immersing it in water. In a portion of intestine inflated, dried, and laid open longitudinally, they are seen as transverse crescentic folds or ridges, wider in the middle, and tapering at either end. Each extends about half or two-thirds around the interior of the tube; the longest are about two inches in length, and one-third of an inch wide at their broadest part, but most of them are smaller; the larger and smaller ones alternate; unlike the rugæ of the stomach, they are permanent, and not obliterated by distension; they do not contain any of the circular muscular fibres, as the pyloric valve does. They begin in the duodenum, about one inch below the pylorus; in the lower part of the duodenum, they are very large, and succeed each other closely; about the middle of the jejunum, they begin to get smaller and wider apart; in the lower half of the ileum, they become less distinct, and in the lowest part of that intestine, they are altogether wanting. The *mucous* membrane of the small intestine, which also covers the *valvulae conniventes*, is specially characterised by being everywhere closely beset with an immense number of minute thread-like processes, called *villi*; when immersed in water, these stand up and produce a flocculent appearance, resembling the pile of velvet; hence this mucous membrane has been termed *villous*. It also contains the intestinal glands, to be presently described, and other glands to be noticed, with the lacteals, in the section on Absorption. The nerves of the small intestine are derived immediately from the sympathetic system; on their finest branches in the submucous areolar tissue, are found multitudes of the microscopic ganglia, elsewhere noticed (vol. i. p. 325); others exist between the circular and longitudinal muscular layers (Meissner, Auerbach).

The movements of the small intestine, depending on the contraction of its longitudinal and circular fibres, afford the most perfect example of *vermicular* or *peristaltic* movements. They consist, in the healthy state, of slow, successive, wave-like contractions, chiefly of the circular fibres, from the upper to the lower part of the intestine. They are noticeable in very emaciated persons during life, but are powerfully ex-

cited by exposure of the intestines to the air, especially when the abdominal aorta has been tied; they continue for a short time after death, and even when the intestine is removed from the body. By narrowing the small intestine, they urge gently onwards from its upper to its lower end, the pulpy mixture of the alimentary substances and digestive juices, gently compressing these soft materials against the mucous membrane, passing them on, over the numerous valvulæ conniventes, and so undoubtedly aiding in absorption. The progressive contractions of the longitudinal fibres, open and unfold the coils of the intestine, which otherwise might arrest the progress of its contents.

The peristaltic movements of the intestines are influenced, both through the cerebro-spinal and sympathetic nervous systems; this is shown by experiments on animals, by irritation of the solar plexus, spinal cord, and brain, and also by the peculiar effects of emotions on these movements; they are accelerated by moderate stimulation, and retarded, or arrested or inhibited, by more powerful irritations. But, as they may continue after the intestine is removed from the body, it is possible that they are usually excited, either by the direct stimulation of the muscular fibres, or else, in a reflex manner, through the intervention of the minute nervous ganglia found in the submucous tissue, and in the circular and longitudinal muscular layers. The stimuli which excite these motions are, in either case, the digested food, and the various digestive fluids; of the latter, the bile is the most stimulating, and its importance as a regulator of the action of the alimentary canal, is well known.

Besides these intrinsic movements, the small intestine is acted upon jointly by the diaphragm and the abdominal muscles, which subject it to various degrees of pressure, and more or less alter its general position in the abdomen; such movements must aid in urging onwards the contents of the intestine. It has been estimated that the time occupied in the descent of the digested food along the small intestine, is about three hours.

The *large intestine*, fig. 89, *c* to *r*, extends from the small intestine to the termination of the alimentary canal. It measures usually about five or six feet, *i.e.* about one-fifth of the whole length of the intestinal canal. Though much shorter than the small intestine, it is considerably wider, measuring from $1\frac{1}{2}$ to $2\frac{1}{2}$ inches in width, being widest at its commence-

ment, and gradually narrowing as it descends. It pursues a remarkable course; commencing in the right iliac fossa, where the small intestine opens into it, it ascends along the right side to the under surface of the liver, then passes across, between the umbilicus and the pit of the stomach, to the left side of the abdomen, whence it descends to the left iliac fossa, and, having described a double or *sigmoid* curve, enters the pelvis, through which it passes down, supported by the sacrum and coccyx. The large intestine is more or less arbitrarily divided into three parts; the first part named the *cæcum*, *c*, with its *vermiform appendix*; the second part, the *colon*, *co* to *co*, again subdivided into the *ascending*, *transverse*, *descending colon*, and *sigmoid flexure of the colon*; and the third part, or terminal portion, named the *rectum*, *r*.

The ileum, *i*, enters the inner or left side of the large intestine, *c*, a short distance above the commencement of the latter, which forms, below the point of entrance, a pouch-like portion, about two inches in length, constituting the *cæcum*, so named because it is a *blind* pouch or cul-de-sac, fig. 92, *c*.

Projecting from the lower and back part of the *cæcum*, is a narrow, coiled, and tapering, tube, about 4 inches in length, and about as thick as a worm, hence named the *vermiform* or worm-like *appendix*, fig. 92, *a*. It communicates with the *cæcum* by an opening, protected by a membranous ridge; its outer end is closed. It may be regarded as a part of the *cæcum* arrested in its growth, and is the homologue of the long *cæcum* found in Mammalia generally, the orang-outang, chimpanzee, and wombat being, however, exceptions.

The *cæcum*, and the ascending, transverse, and descending colon, with its sigmoid flexure, are distinguished from the small intestine, and also from the rectum, by their peculiar sacculated form. The *sacculi* of these parts, are arranged in three longitudinal rows, separated from each other by three intermediate bands. Their presence depends upon a peculiar arrangement of the coats of the intestine. These, as in the small intestine, are four in number, viz. proceeding from without inwards, the serous, the muscular, the areolar, and the mucous coats. The *serous* or *peritoneal* coat, is complete in only certain portions of the great intestine, viz. in the transverse part of the colon, the sigmoid flexure, and the upper part of the rectum; whilst the *cæcum*, the ascending and descending colon, and the lower part of the rectum, are

closely fixed behind, and therefore receive only a partial covering from the peritoneum. The *muscular* coat consists, as usual, of external longitudinal and internal circular fibres. On the vermiform appendix, both sets of fibres form uniform layers. On the sacculated pouch of the cæcum, and throughout the whole length of the colon, however, the longitudinal fibres, thinly scattered over the sacculi, are chiefly collected into three long bundles, which form the three longitudinal bands between the sacculi. These bands, indeed, are *shorter*, from end to end, by nearly one-half, than the intermediate part of the intestine, which accordingly is puckered, and projects inwards in the form of sharp crescentic ridges between the dilated parts which form the sacculi. These sacculi become smaller and more scattered on the sigmoid flexure of the colon. On the rectum, the longitudinal fibres speedily form a thick stratum, evenly distributed over the whole circumference of the intestine, so that the sacculi disappear. The circular fibres cover the whole surface, but are accumulated in greater numbers on the ridges between the sacculi. Upon the rectum, however, they soon form a thick and uniform layer; the lower portion of this is particularly well developed, constituting the *internal sphincter muscle*, which constricts the lower part of the bowel, and assists the external sphincter muscle, situated beneath the skin, around the aperture of the intestine, in keeping the bowel closed. The *areolar* or submucous coat of the large intestine, is attached loosely to the muscular coat, but more intimately to the mucous membrane; it is sacculated, and helps to maintain the form of the intestine; it supports the tender mucous coat, and furnishes a stratum, in which the bloodvessels, lymphatics, and nerves, ramify. The *mucous* coat, unlike that of the small intestine, follows strictly the form of the intestinal canal itself; for it is not thrown into proper folds, like the valvulæ conniventes, but only follows the concentric ridges between the sacculi. Moreover, it differs from the mucous membrane of the small intestine, in being somewhat thicker and paler, and in being perfectly smooth and entirely destitute of villi. In the cæcum and colon, it is of a greyish yellow colour, but in the rectum, it is darker, thicker, more vascular, and more loosely connected with the muscular coat. Its glands will be presently described. The nerves belong to the sympathetic system; in the submucous coat, their fine branches present microscopic ganglia, which are also found outside the muscular coat. The

movements of the large intestine are not retarded by irritation of the splanchnic nerves.

At the junction of the lower end of the ileum, fig. 92, *i*, with the cæcum, *c*, and colon, *co*, there is found a very perfect valve, the *ileo-cæcal* valve, or valve of Tulp or Bauhin, composed of two semi-lunar segments, having their free edges directed towards the large intestine. The end of the ileum is somewhat flattened on its upper and under aspects, and is here inserted into the left side of the large intestine. The flattened part of the small intestine, carries in, with it, the side of the large intestine, and so forms the segments of the valve,

Fig. 92.

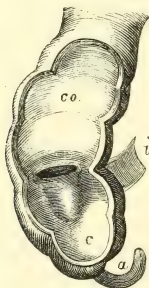


Fig. 92. The cæcum, and the commencement of the ascending colon, laid open in front, to show the ileo-cæcal or ileo-colic valve, at the junction of the small and large intestines. *c*, the cul-de-sac, named the cæcum, or blind intestine. *a*, vermiform appendix of the cæcum. *co*, part of the ascending colon. *i*, A piece of the ileum, or small intestine, entering the side of the large intestine, between the cæcum and colon, by a horizontal transverse fissure, bounded, above and below, by the crescentic segments of the ileo-cæcal or ileo-colic valve. Much reduced in size.

which consist therefore of the coats of both intestines, excepting, however, the longitudinal muscular fibres and the peritoneal tunic. If the latter be carefully divided where it passes from one intestine to the other, the inserted part of the small intestine, may be drawn out from the side of the large intestine, when the two segments of the ileo-cæcal valve disappear, and the small intestine seems to open widely into the side of the large intestine. In the natural condition, the segments of this valve are placed one above the other, and leave, between their free edges, a narrow, nearly horizontal,

slit, leading from the small into the large intestine. Each segment contains circular muscular fibres, areolar tissue, and two layers of mucous membrane, continuous with each other at the free edge of the segment. The mucous membrane of the surface turned towards the ileum, is covered with villi; whilst that turned towards the large intestine, is destitute of those processes.

Notwithstanding the active absorption which takes place along the whole length of the small intestine, its contents retain a pulpy consistence. By the peristaltic action of the circular muscular fibres, they are pressed through the slit-like opening between the segments of the ileo-cæcal valve, having passed which, they are received into the pouch of the cæcum, which now supports their weight, whilst the lateral position of the valve relieves it from pressure. Once having passed the valve, no force exerted upon the intestinal contents, can ever return them into the small intestine, the valve-segments, owing to the elasticity and muscularity of all the parts, meeting closely together under every change of dimensions. Even after death, when these parts are removed from the body, water, poured into the colon, is, owing to the closure of the valve-segments, completely prevented from passing into the ileum. In the cæcum, the still pulpy residue of the processes of digestion and absorption, undergoes further inspissation, perhaps also further digestion. By the combined and comparatively slow peristaltic action of the longitudinal bands between the sacculi, and of the circular fibres spread over the sacculi themselves, it is pressed upwards into the ascending colon, and, in like manner, onwards from sacculus to sacculus of the ascending, transverse, and descending colon, and, yet more slowly, through the sigmoid flexure of the colon into the rectum, acquiring, by gradual absorption, as it descends, its final state of inspissation, before it is expelled from the body. Undue pressure, or weight, is prevented by the sigmoid curve of the intestine. The external and internal sphincters, which close the rectum below, are kept contracted, in a reflex manner, by the action of the spinal cord. In defæcation, these muscles are relaxed, whilst the intestine above contracts, the action being aided by expulsive efforts on the part of the abdominal and expiratory muscles generally, the diaphragm being fixed after closure of the glottis. The fibres surrounding the cardiac opening of the stomach, must also close that aperture simultaneously.

Vomiting.

In the ordinary exercise of their functions in the digestive process, the œsophagus, the stomach, and the intestinal canal, manifest, as we have seen, movements of the so-called *peristaltic* kind, due to successive wave-like contractions of their muscular walls, excited, partly through the nervous system, but also, especially in the case of the intestines, by the direct stimulation of the food upon them. But, under certain conditions, an undue local stimulation of the muscular fibres, or some wider irritation, operating through the nervous system, excites these organs to reversed, or so-called *anti-peristaltic*, action, often accompanied with powerful associated movements of the abdominal muscles, and with certain peculiar states of the diaphragm and muscles of respiration generally, so producing the acts of *eructation*, *regurgitation*, *retching*, and *vomiting*.

The *eructation* of gaseous matters, depends chiefly on the contraction of the walls of the stomach and œsophagus, aided slightly by that of the abdominal muscles and the diaphragm.

The act of *vomiting* is a more general, and powerful movement, and often involves a contraction of the small intestines; but it depends essentially on a similar mechanism. Though an exceptional phenomenon, and, in disease, often a serious or fatal symptom, it is, in many instances, beneficial, relieving the stomach of indigestible, irritating, or poisonous substances, expelling from it morbid secretions, or even inducing a state of exhaustion, in some way favourable to ultimate recovery. *Retching* is unsuccessful vomiting.

Regurgitation is performed by the same mechanism as vomiting; but its effect is limited to the expulsion of small portions only of the contents of the stomach. There are persons who possess a sort of power of *rumination*, swallowing their food half chewed, and, after a time, returning it to the mouth, where it is fully masticated, and then re-swallowed.

The actual contraction of the stomach, in *vomiting*, is sometimes felt; indeed, it has been witnessed. In a man, in whom the entire stomach protruded through a wound of the abdomen, forcible and repeated contractions of this organ, were observed to continue for half-an-hour, till it was entirely emptied of its contents (Lepine). As a preliminary condition to the inverted action of the fibres of the stomach

generally, the pyloric muscular ring contracts tightly, whilst the oblique fibres surrounding the cardiac orifice are always, and necessarily, relaxed; otherwise the contents of the stomach could not enter the œsophagus. The ineffectual attempts to vomit, sometimes noticed, before the actual expulsion of the contents of the stomach, are due to the contraction of these cardiac fibres, which contraction ordinarily serves to retain the contents of the stomach, during any violent effort on the part of the abdominal muscles. The relaxation of these fibres, in vomiting, is immediately followed by an antiperistaltic action of those of the œsophagus, movements which have been observed in the horse, after the injection of tartar emetic into its veins, and have been found to continue even when the œsophagus is separated from the stomach. It has been suggested, that the upward propulsion of the contents of the stomach or intestines, and of matters rising in the œsophagus, is due to a downward or peristaltic action meeting with resistance, and producing a central, or so-called axial current upwards (Brinton); but this explanation is not generally adopted, and antiperistaltic movements certainly occur in animals.

The influence of the abdominal muscles in vomiting, is obvious, and, indeed, Magendie suggested, that these muscles and the diaphragm were alone concerned in this act, the stomach being, as it were, passive, and merely compressed by the descent of the diaphragm, and the backward movement of the abdominal muscles. This view is supported by Béclard and Budge. The administration of tartar emetic, to an animal, or its injection into the veins, was said, by Magendie, never to produce contraction of the stomach. He found that, on drawing this organ out of the abdomen, no vomiting occurred; but, as soon as it was replaced in its normal situation, the action of the abdominal muscles, or the pressure of the hand, immediately produced vomiting; even after removal of the abdominal muscles, so as to leave only the linea alba, or the tendinous structure in the middle line of the abdominal walls, the descent of the diaphragm, according to that observer, still emptied the stomach. Moreover, on removing the stomach, and supplying its place by a bladder attached to the œsophagus, the contents of the former were forced upwards by the contraction of the abdominal muscles. It is, however, generally believed, that these experiments merely prove, that the abdominal muscles are powerful agents in

expelling the contents of the stomach into the œsophagus, just as they assist, most materially, in the expulsion of the contents of the other hollow viscera. They do not show a completely passive condition of the stomach itself, which organ, as just stated, has been seen to be able to empty its own contents. In experiments on animals, when the abdomen is opened, the movements of the stomach are frequently so feeble and rapid, that they might escape observation.

It was supposed by Magendie, that the diaphragm is actively concerned in vomiting, undergoing a movement of *descent*; but, the associated acts necessary to vomiting, are *expiratory*, and the descent of the diaphragm is an inspiratory movement (Marshall Hall). At the moment of vomiting, the diaphragm, though more or less contracted, is certainly *fixed*; for, previous to each act of vomiting, a powerful inspiratory effort occurs, and the diaphragm of course descends; but the glottis is then closed, and any further movement, on the part of the diaphragm, is thus prevented, so that it probably remains passive in vomiting.

During vomiting, as in the second stage of deglutition, certain muscles draw the soft palate across the pharynx, and prevent the vomited substances from passing into the posterior nares; but when the abdominal muscles act very powerfully, these are sometimes ejected through the nose.

As elsewhere mentioned, vomiting is a *reflex* act, the pneumogastric nerves being the afferent nerves, the medulla oblongata and cord, the excitable centres, and the nerves of the various muscles concerned, the efferent nerves. Sometimes it is *excito-motor*, and induced by a *local* stimulus, applied to the interior of the stomach itself, such as indigestible food, medicines, poisons, or diseased secretions; it may also be due to morbid irritability of this organ, from inflammation, ulceration, or other disease; or the cause of irritation may be distant, as in the intestines or some other part. In certain cases, as in sickness produced by a blow on the eye-ball or on the shin, by strangulation of the intestine, or by a calculus in the kidney, the reflex act is *sensori-motor*, or accompanied by sensations which are always of a painful kind. The nausea and vomiting caused by tickling the fauces, by disagreeable tastes and odours, or by sickening sights, are likewise *sensori-motor* in their character. Sea-sickness is also an example of *sensori-motor* vomiting. *Emotional* causes may likewise excite this act. Emetic medicines, which operate just as readily

when injected into the veins, as when introduced into the stomach, probably act directly on the reflex nervous centres concerned in vomiting; but they may operate on the extremities of the afferent nerves of the stomach. These are the pneumogastric nerves, irritation of which causes, amongst other results, contraction of the muscles of the abdomen, and vomiting. In the vomiting, named *cerebral* vomiting, which occurs after concussion of the brain, and in certain diseases of that organ, the cause of irritation is central. In some individuals, vomiting can be performed voluntarily, this power being either natural, or else acquired by practice.

It is said that the act of vomiting but seldom occurs in the horse; and it has been attempted to explain this, by reference to the structure of the cardiac end of the stomach; but it would seem rather to be due to the very slight susceptibility of that animal to the action of emetic medicines.

THE DIGESTIVE FLUIDS.

The chemical processes concerned in the function of digestion, consist of peculiar reactions between the food and the various secretions of the alimentary canal.

The digestive fluids, which are added to, and act chemically on, the food in its progress through the alimentary canal, are as follow:—first, the fluids of the mouth, consisting of the *mucus* secreted by the mucous membrane and glands of that cavity, and the *saliva*, the product of the three pairs of salivary glands, named the *parotid*, *submaxillary*, and *sublingual* glands; secondly, the secretion of the stomach, named the *gastric juice*, formed by minute gastric glands, or follicles, embedded in the mucous membrane of that organ; thirdly, the *bile* secreted by the liver, and poured into the duodenum; fourthly, the *pancreatic juice* secreted by the pancreas, and also added to the food in the duodenum; and lastly, the mucus and the *intestinal juices*, secreted by the mucous glands, and by the so-called tubuli, which exist in vast numbers in the mucous membrane of every part of the small and large intestines. Each of these fluids exercises a special transmutation on one or more of the proximate constituents of the food, the tendency of such changes, being to convert those constituents, from an insoluble and unabsorbable condition, into a state of solution, or into a state in which they can be absorbed, that being the ultimate object of the digestive process.

Sources and Composition of the Buccal Mucus and Saliva.

The *mucous glands* of the mouth are named, according to their position, *labial*, *buccal*, *molar*, *palatal*, and *lingual*. These are chiefly compound racemose glands, forming rounded masses beneath the mucous membrane, and opening into the mouth by their proper ducts. At the base of the tongue, are a few simple follicles, and some follicular depressions, having little closed sacs in their walls, like the follicles of the tonsils. The tonsils themselves probably also furnish some mucous secretion. Beyond the mouth, the pharynx possesses numerous simple follicles, and its upper part, compound racemose glands. Their secretion lubricates the parts, and also the surface of the food. It may likewise aid the saliva in its chemical action. Throughout the whole length of the œsophagus, and especially in a circular group around its lower end, there are also numerous compound mucous glands, which perform similar offices.

Of the three pairs of *salivary glands*, the *parotid glands* are by far the largest, weighing from 5 to 8 drachms each. They are placed one on each side of the face, between the ear (*παρά*, near, *οὖς*, *ὠρός*, the ear) and the lower jaw, which they overlap, being there supported by their ducts and blood-vessels, and by a strong fascia. The facial nerves pass through the glands. The principal mass of each gland occupies the position above indicated, and likewise penetrates amongst the muscles and vessels of this region; but a secondary or *accessory* portion, *sociæ parotidis*, extends forwards along the excretory duct. This canal, named the *Stenonian duct*, runs forward from the gland, over the masseter muscle, passes obliquely through the buccinator muscle, and, opposite the second upper molar tooth, opens by a narrow orifice into the mouth. It is about $2\frac{1}{2}$ inches long, and about the diameter of a crow-quill, but its orifice is very minute. The gland itself consists of numerous compressed lobes, held together by the ramified ducts and blood-vessels, and by areolar tissue. The lobes are again divided into lobules, each of which is a minute racemose gland, the branched ducts of which, terminate in vesicles, about $\frac{1}{1200}$ of an inch in diameter, fig. 42, c., each being surrounded by a network of capillaries. The saliva, secreted from the blood into these vesicles, flows along the smaller branches of the ducts, into the main canal or duct of Steno, and is thence poured into the mouth at a place suitable for

moistening the dry food, and for being mixed with the alimentary mass. The *submaxillary* glands are placed, one on each side, beneath the horizontal part of the lower jaw, attached by their ducts and blood-vessels, and supported by the cervical fascia and certain muscles. Each gland is of a roundish shape, and weighs from 2 to $2\frac{1}{2}$ drachms; its structure resembles that of the parotid. Its chief duct, thinner than that of the parotid, is named the Whartonian duct, and is about 2 inches long; it runs forwards between the muscles, beneath the sublingual gland, to the side of the frænum of the tongue, where it opens upon a small eminence close to the duct of the opposite side. These glands, therefore, discharge their saliva, not outside the jaws, like the parotid glands, but inside the lower dental arch, their secretion being pressed up into the mouth by the motions of the tongue. The *sublingual* glands, the smallest of the salivary glands, are somewhat almond-shaped, and weigh each about one drachm; they form two narrow oblong ridges, about $1\frac{1}{2}$ inch long, placed, one on each side, beneath the tongue. Their structure resembles that of the other salivary glands, but, instead of having a common duct, the several lobules open into from eight to twenty ducts, named the Rivinian ducts, some of which, including one large duct named the duct of Bartholin, join the Whartonian duct, as it runs for a certain distance immediately beneath the gland. The saliva from the sublingual glands, flows into the mouth, beneath the tip and sides of the tongue.

The mechanical flow of the saliva into the mouth, is aided by the contraction of the muscles of the tongue and jaw engaged in mastication; on opening the mouth before a looking-glass, and then turning up, and stiffening, the tongue, the saliva is sometimes seen to be ejected a considerable distance, from the orifices of the Whartonian ducts.

The salivary glands all receive branches from the sympathetic nervous system; the parotid glands are likewise supplied by the fifth pair (its auriculo-temporal branch); whilst the sublingual and submaxillary glands receive nervous filaments from the chorda-tympani branches of the facial nerves. The saliva flows intermittently; and its secretion is excited through the nervous system, by the agency of which, the quantity of this and other secretions, is chiefly regulated (Vol. I., p. 333). Thus, the presence of food, especially of dry food, in the mouth, and even the introduction of food into the stomach through a gastric fistula, stimulates the flow of saliva;

salt, vinegar, pepper, and other condiments, and particularly tobacco, and the root of the pellitory of Spain, have a still more powerful effect; these furnish examples of reflex stimulation of the salivary secretion. The afferent nerves concerned, are the gustatory branches of the fifth pair, and the glossopharyngeal nerves; the efferent nerve-fibres are contained in the chorda-tympani branches of the facial nerves, or in the auriculo-temporal branches of the fifth pair. The nervous centres are the submaxillary ganglia, and the cerebro-spinal axis. Besides this, the saliva is excited to flow by ideational or other mental stimuli, such as the sight of food, or even the thought of it. The act of speaking, and also that of vomiting, are preceded by a flow of saliva. Fear diminishes or arrests it. Irritation of the fourth ventricle, and the presence of certain substances in the blood, especially of mercury, likewise increase the flow of this secretion. The effect of mercurialization in exciting a flow of saliva, is specific.

The mode in which the nervous system influences the secretion of saliva, has been elucidated by the interesting experiments of M. Bernard. When the sublingual and submaxillary glands, exposed in an animal, are at rest, little or no saliva being formed, the veins are seen to contain a moderate quantity of dark blood. On now stimulating the glands, in a reflex manner, by the application of vinegar to the tongue, the arteries supplying them dilate, the flow of blood through these vessels becomes quicker, even the veins pulsate, the venous blood is of a bright red colour, and there occurs a copious flow of watery saliva. The afferent nerves concerned in this reflex act, are obviously branches of the gustatory and glossopharyngeal nerves; the efferent fibres are contained in the chorda tympani; for if either this or the facial, from which it is derived, be cut, the active phenomena, above described, all gradually cease, but they are again excited by irritation of the *distal* ends of the divided nerves. If the facial nerve be drawn out from the cranial cavity, irritation of the glossopharyngeal no longer increases the flow of saliva. The efferent nerves of the parotid glands, are said, by Eckhard, to proceed, not from the chorda tympani or facial, but from the auriculo-temporal branch of the fifth pair. As already stated (Vol. I., p. 333), irritation of the sympathetic branches supplying the sublingual and submaxillary glands, has an opposite effect to that of stimulating the fibres of the chorda tympani; the secretion from the glands, then becomes scanty and thick, the

arteries small, the flow of blood through the gland diminished and retarded, and the venous blood dark. To explain these opposite phenomena, it is assumed that the sympathetic nervous centres cause a contraction of the muscular coats of the smaller arteries; whilst the cerebro-spinal centres inhibit this power, and so induce a relaxed condition of the arterial coats. The efferent effect, conveyed through the chorda tympani nerve-fibres, is therefore not *motor*, but of a special kind, controlling, or inhibiting, the action of the sympathetic nerve-fibres and centres. This example will suffice to illustrate the mode in which secretion generally, is believed to be influenced through the nervous system. Irritation of the sympathetic nerves does not alter the quality, but only lessens the quantity, of the secretion of the parotid glands. According to Eckhard, great numbers of mucous corpuscles, exhibiting intrinsic movements, like those of the *Amœba*, are found in the viscid secretion of the sublingual and submaxillary glands, after irritation of their sympathetic nerves; such corpuscles, but in smaller number, exist, as we shall see, in ordinary saliva.

The chemical composition of the saliva is, according to Dr. Wright, as follows:—

Water	98·81	. . . = 98·81
Ptyalin, or Salivin	·18	} Solids . = 1·19
Fatty matter	·05	
Albumen with Soda	·17	
Mucus	·26	
Ashes	·41	
Loss	·12	
	<hr/> 100·	<hr/> 100·

The saliva, thus constituted, is a transparent watery fluid, destitute of smell; its specific gravity varies from 1002 to 1008. Besides fine granular particles, mucous corpuscles, derived, for the most part, from the lingual and tonsillar glands, and epithelial cells detached from the mouth, the saliva contains the so-called *salivary corpuscles*, spheroidal nucleated cells, somewhat resembling the white blood corpuscles, which undergo *Amœba*-like changes in form, and exhibit a molecular movement in their interior.

The quantity of saliva secreted in twenty-four hours by all the glands, has been estimated at from 1 to 3 lbs.: but it differs according to the nature of the food, and the intervals between the meals. Its flow is increased by mastication,

but is arrested by the cessation of that movement. The saliva from the parotid gland, is very thin and watery, and becomes more abundant during mastication; that from the submaxillary, and especially from the sublingual gland, is more viscid, and flows more constantly, for purposes of speech. The parotid glands, when active, are said to secrete from eight to ten times their own weight in one hour. When first secreted, and especially during active secretion, the saliva is alkaline; that of the submaxillary gland is less so than that of the parotid. In fasting, the moisture of the mouth is nearly neutral, or even acid, at that time consisting probably almost entirely of mucus. The *ptyalin* or *salivin*, the most important constituent of the saliva, is an albuminoid substance. Of the salts, the tribasic phosphate of soda is probably the cause of the alkalinity of the secretion; besides this, there are found chlorides of sodium and potassium, sulphate of soda, phosphates of lime and magnesia, and oxide of iron. The tartar of the teeth is formed by a deposit of these earthy salts, mixed with mucus, and the remains of bacteria or vibrios; it contains 20 per cent. of animal matter. Urea has also been found in the fluids of the mouth, and traces of ammonia, the results of decomposition. Thus far, the salts of the healthy saliva resemble those of the blood; but it contains a peculiar and remarkable salt, named the *sulphocyanide of potassium*, which strikes a deep red colour, with a solution of a persalt of iron.

Source and composition of the Gastric Juice.

When the soft pulpy mucous membrane of the stomach is examined under a moderate magnifying power, it presents a delicate honeycomb appearance (fig. 93), caused by numerous, shallow, hexagonal, or polygonal, depressions, named the *cells* or *alveoli* of the stomach; near the pylorus, these measure $\frac{1}{100}$ th of an inch in width, but elsewhere are smaller and less distinct, measuring only $\frac{1}{200}$ th to $\frac{1}{350}$ th of an inch. Between the alveoli, are slightly elevated ridges, upon which, especially near the pyloric end of the stomach, are minute processes, which somewhat resemble villi, and are more distinct in the infant. No lacteals, however, have been detected in them. At the bottom of the alveoli are clusters of minute spots (fig. 93), which are the orifices of tubular follicles. These follicles, called the *gastric glands* or *tubuli*, secrete the gastric juice; they are arranged, side by side, in little groups (fig. 94), perpen-

dicularly to the surface of the membrane, and form almost its entire substance. At the pyloric end of the stomach, where the mucous membrane is thickest, the tubuli are the longest, measuring nearly $\frac{1}{20}$ th of an inch in length; towards the cardiac end, where the mucous membrane is thinnest, they are less thickly set, and become gradually shorter, measuring only $\frac{1}{60}$ th of an inch in length; their average diameter is about $\frac{1}{360}$ th to $\frac{1}{500}$ th of an inch, the orifices, *c*, being somewhat narrower. Each follicle is somewhat dilated, or flask-shaped, at its deeper or blind end; the larger follicles are sometimes convoluted or varicose, and sacculated at the blind end, or

Fig. 93.

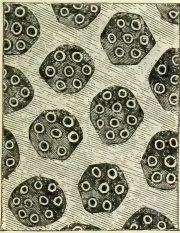


Fig. 94.

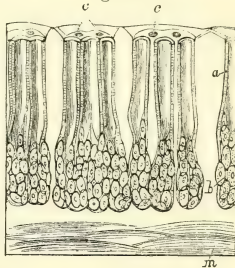


Fig. 93. Minute portion of the surface of the mucous membrane of the human stomach, showing the polygonal depressions or alveoli, with the elevated ridges between them. At the bottom of the alveoli, are seen the open mouths of clusters of the tubuli of the stomach, or gastric tubuli. Magnified 60 diameters. (After Boyd.)

Fig. 94. Perpendicular section through a small piece of the mucous membrane of the stomach, to show the clusters of the gastric tubuli. *a*, neck of a single tubule. *b*, dilated end or fundus, filled with glandular epithelial cells. *c*, orifices of the tubuli, at the bottom of the alveoli. *m*, muscular bundles of the muscular coat. (After Kölliker.) Magnified 40 times.

even subdivided into two, or, sometimes, as in the pyloric portion of the stomach, into as many as six or eight short sacculated tubuli. These tubuli consist of extensions of the gastric mucous membrane. The upper third of each tubule, next to its orifice, is lined by columnar epithelial cells (fig. 95, *a*), arranged perpendicularly on the basement membrane. This epithelium is continuous with that at the bottom of the alveoli, and on the interalveolar ridges, and indeed is similar

to that lining the stomach generally. In the lower two-thirds of each tubule, the epithelium changes its character, being composed of soft, roundish, oval, or compressed nucleated cells, *b*, which, very much larger than the cylindrical epithelial cells, and distended with granular matter, almost or completely block up the cavity of the tubule. These soft epithelial cells are named the *peptic* cells, because in, or by, them, the gastric juice, or, at least, its characteristic animal substance, called *pepsin*, appears to be formed. Some of these cells are present as microscopic elements of the gastric juice. The tubuli, which are said to number about five millions, are sometimes

Fig. 95.

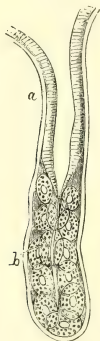


Fig. 95. Single gastric tubulus, or peptic gland, more highly magnified. *a*, neck of the tubule, lined with columnar epithelium. *b*, dilated lower end, or fundus, of the tubule, filled with oval nucleated glandular epithelial cells, or peptic cells. Magnified 70 diameters.

named the *peptic glands*. They are surrounded by a fine capillary network; minute arteries and veins pass up and down between them, and end in a capillary plexus on the bottom of the alveoli, and on the interalveolar ridges. The unstriped muscular fibres found in the submucous coat, are placed immediately beneath these glands, and probably assist in expelling their secretion.

Besides these proper gastric or peptic glands, there are found, especially near the pylorus, clusters of larger simple and compound *mucous* glands, which are lined throughout with cylindrical epithelium, and are supposed to secrete gastric mucus.

In certain conditions of the stomach, especially during and after digestion, and also in irritation and inflammation of this organ, and nearly always in the stomachs of infants, numerous small, milky-white, elevated spots are seen scattered over the mucous membrane. These consist of lenticular *closed* sacs, not opening on the surface; they are filled with a white, semi-fluid and finely granular substance. They resemble the closed sacs of the tonsils, and of the so-called solitary and agminated glands of the small intestine, to be hereafter noted; like them, they are now considered to be appendages of the absorbent system. The lymphatics of the stomach form a fine net-work near the surface of the mucous membrane, and coarser plexuses in the submucous coat, all intimately connected together.

The *gastric juice*, during the digestive process, or under the excitement of condiments, small stones, and other irritant bodies, exudes from every part of the mucous membrane of the stomach, which then assumes a bright red hue. The secretion pouring from the tubules, oozes from the alveoli in minute drops, which speedily run together, and cover the whole mucous membrane. This has been seen by Dr. Beaumont and others, in the case of Alexis St. Martin, a Canadian voyageur, the interior of whose stomach was exposed by a gunshot injury.

The condition of the stomach, and the formation of the gastric juice, as of other secretions, are influenced by the nervous system. It was shown, by Dr. John Reid, that the division of both pneumogastric nerves, in the neck of a dog, in the first instance, arrested digestion; but that, if the animal lived sufficiently long, the process might be restored; for then, generally, the state of emaciation, which followed the experiment, was removed, acid and partly digested food was vomited, and absorption and chylicification took place. This restoration of function was not due to reunion of the divided nerves, for portions of the nerves were removed, or care was taken to keep the cut ends apart. Bernard also found, that, on division of these nerves, the stomach became pale, its walls relaxed, and the formation of gastric juice was instantly arrested, digestion being thus stopped. On the other hand, galvanising these nerves increased the gastric secretion. According to Longet, however, the pneumogastric nerves are rather the motor nerves of the stomach, their division, as he believes, chiefly affecting the movements of that organ; for he found, that milk, introduced into the stomach one or two

days after the operation, always became coagulated; whilst, although large portions of food were only acted upon on the surface, owing to the paralysis of the muscular fibres, and the necessary absence of the churning movements of the stomach, yet small portions were actually digested. By Budge, it is believed, that the very decided effect of division of these pneumogastric nerves on digestion, noticed by Reid and Bernard, was owing to those nerves having been cut in the neck, so as to interfere with respiration, and thus disturb the whole economy; for, he observed that, on dividing them in the rabbit, close to the cardiac orifice of the stomach, no interference with the appetite, the gastric secretion, or digestion, occurred. Although, therefore, the secretion of the gastric juice appears to be influenced by the cerebro-spinal nervous system, through the pneumogastric nerves, it cannot be said to be dependent upon it. The effects of mental emotion, in arresting digestion, sufficiently prove this influence.

It has been stated by Bernard, that galvanism applied to the sympathetic nerves of the stomach, causes an immediate cessation of its secretion, this effect being the reverse of what happens, when the pneumogastric nerves are so stimulated. If these two results are confirmed, they would correspond with those already detailed (p. 56), as to the effects of stimulation of the sympathetic nerves and the chorda tympani, on the secretion of the sublingual and submaxillary glands. Neither division of the splanchnic nerves, nor section of the pneumogastrics *upon* the stomach, that is to say, after the latter have received the fibres from the former nerves, has appeared to interfere much, or at all, with the gastric secretion (Schiff and others); even the celiac plexus, and the neighbouring ganglia, have been removed without permanent effect (Budge). It would seem impossible, however, in any such experiments, to remove, or divide, *all* the sympathetic nerves of the stomach. Finally, the influence of this part of the nervous system, on the gastric secretion, is uncertain; and it is not yet shown that the secretion is either arrested by, or depends on, the sympathetic system.

The quantity of the gastric juice secreted, appears to be enormous. In dogs, the daily quantity has been calculated as $\frac{1}{20}$ th (Corvisart), or $\frac{1}{10}$ th (Lehmann), part of the weight of the body; the latter ratio would give 14 lbs., in a man of 140 lbs. weight, a quantity equal to rather more than 11 pints daily. That this estimate, however large, is not extreme, is

shown by the fact that, in a case of gastric fistula, in a woman, the estimated daily quantity was $30\frac{1}{2}$ lbs. av., the weight of her body being 116 lbs. From observations on dogs, having artificial gastric fistulæ, the secretion appears to be less abundantly excited by mechanical, than by chemical or special irritants, such as salt or pepper; acid food excites a less abundant flow than food made slightly alkaline; but alkali in the solid state, induces an abundant secretion of mucus. Too powerful mechanical irritation has a similar effect, lessening, or arresting, the secretion of proper gastric juice, and, in both cases, vomiting, and the passage of bile into the stomach, may take place. Powerful chemical irritants arrest digestion, and cause signs of inflammation. The effect of cold water, or ice, is, after first causing the gastric membrane to be pale, ultimately to increase the flow of blood to it, and to excite a very active secretion; ice, in larger quantity, causes shivering, and delays digestion. A high temperature, even a small quantity of boiling water, produces collapse and death within four hours, causing redness, turgescence, and ecchymosis of the mucous membrane (Bernard). Dr. Beaumont found that, on injecting into the human stomach only 2 ozs. of water at 50° , the temperature of this organ was depressed to less than 70° , and required more than half-an-hour to regain its normal standard, viz. about 100° .

The specific gravity of the gastric juice, in Man, is 1002·5; in the dog, 1005. The quantity of solids is about ·5 per cent. It is a colourless, or pale yellow, transparent, slightly viscid, and strongly acid fluid, having a faint smell. It resists putrefaction, and is rendered turbid on boiling. Its composition, mixed with a little saliva, is as follows (Schmidt):—

Water	994·4
Pepsin, with other organic matter.	3·2
Salts	2·2
Free hydrochloric acid	·2

1000·

The gastric juice of the dog, contains ten times as much free acid, and five times as much organic matter; that of the sheep, six times as much acid, and a little more organic matter; that of the horse, is somewhat more concentrated.

The small quantity of solid matter in the gastric juice, is remarkable, considering its extremely active powers. The *pepsin*, its characteristic constituent, is a neutral, albuminoid,

substance, slightly soluble in water, forming, on evaporation, a greyish viscid mass, and having a strong affinity for acids. It is precipitated by tannin, acetate of lead, caustic alkalies, alum, and alcohol. The saline matters consist chiefly of alkaline and earthy chlorides and phosphates. A small amount of lactic acid exists in the gastric juice, but whether as a product of secretion, or of decomposition, is not certain; by Bernard and others, it is even believed to be the special acid of the gastric juice. Acetic, butyric, and other volatile acids are certainly the result of changes in the food. The presence of free hydrochloric acid is undoubted, inasmuch as chlorine is found in the gastric juice in larger quantity than the bases which could combine with it; and moreover, this acid has been obtained by the method of dialysis, and therefore independently of chemical decomposition (Graham). Its existence affords a singular example of the liberation of a mineral acid from its strongly combined base, by an organic process in the living animal economy. The source of this acid is probably chloride of sodium, or common salt; and the seat of its decomposition, like that of the formation of the pepsin, is probably the soft glandular epithelial cells, or peptic cells; but it has been suggested, that it may be secreted by the columnar epithelial cells of the upper part of the tubuli and gastric mucous membrane generally (Brinton). It is supposed by Brücke, that the pepsin is neutral when contained in the peptic cells, and becomes acidified only after its escape from these cells; for the pepsin obtained from the gastric mucous membrane of the animal, after its acidity has been removed by washing, is neutral. It has also been shown by Bernard, that, whereas the introduction of lactate of iron, and ferrocyanide of potassium into the blood of a living animal, produces no blue colour in the blood, tissues, or secretions generally, nor even in the gastric glands, yet the surface of the mucous membrane of the stomach is stained blue. Other parts of the body, moreover, become blue on the application of an acid. This experiment, therefore, also favours the supposition that the acid of the gastric juice is formed near, or at, the surface. It is uncertain whether the separation of the hydrochloric acid, is a direct result of an act of secretion by secreting cells, or whether it is a secondary product of a decomposition, induced by the action of some other intermediately formed free organic acid. The quantity of solid matter in the gastric juice, and the relative amount of organic and saline consti-

tments, differ in different animals. It is universally acid, but the nature of the acid, as well as that of the organic peptic agent, may vary in certain cases, according to the species, age, and diet of the animal. When the stomach is at rest, its mucous secretion is neutral or alkaline, semi-opaque, and more viscid than the gastric juice.

Source and Composition of the Bile.

The *liver* is a solid organ of a dark reddish brown colour, measuring 10 or 12 inches from side to side, about 7 inches from front to back, and about 3 inches in thickness at its posterior margin, its anterior edge being, however, thin. Its average bulk has been differently estimated at 88 or 100 cubic inches; its weight varies from 50 to 60 ounces. It is the largest secreting gland in the body, and, with the exception of the lungs, occupies more space than any other organ. It secretes the bile, the importance of which office is shown by the fact, that the liver is found in all the Vertebrate, and in most of the non-Vertebrate animals.

The substance of the liver has a sp. gr. of 1050 to 1060. It has an acid re-action; its composition, in Man, in 100 parts, is said to be as follows (Beale). The extractive matters mentioned include the amyloid substance named glycogen, a certain quantity of sugar, with traces of inosite, hypoxanthin, xanthoglobulin, urea, and uric acid.

Water	68.58	
Fatty matters	3.82	} Total solids 31.42
Albumen	4.67	
Extractive matters	5.40	
Alkaline salts	1.17	
Earthy salts33	
Vessels, &c., insoluble in water	16.03	

 100.

The liver is placed in the upper part of the abdomen, beneath the diaphragm, reaching from back to front, and from the right side partly over into the left. Its upper surface is smooth and convex, and is adapted closely to the diaphragm. Its thick posterior border rests on the pillars of the diaphragm and on the vertebral column, being hollowed out opposite the latter, and presenting also a deep notch for the ascending vena cava. The thin anterior border is concealed, in the recumbent posture, by the lower ribs and their

cartilages, but descends a little below these parts, in standing, especially during inspiration, when the diaphragm descends (see fig. 13). This border is slightly notched, a little to the left of the middle line. The right border of the liver, nearly as thick as its posterior border, descends lower than the left, and is in contact with the diaphragm; the left border, thinner even than the anterior margin, extends upwards to the cardiac end of the stomach. The under surface, fig. 96, is concave and very uneven, presenting various slight depressions, where it touches the stomach, the duodenum, the bend of the ascending and transverse colon, the right kidney, and its suprarenal capsule; this surface is also marked by special fossæ or fissures for the lodgment of the gall-bladder, *g*, and for the entrance and exit of bloodvessels, lymphatics, nerves, and ducts.

The greater part of the surface of the liver, is covered by the peritoneum, by which its slight changes of position in the abdomen, are facilitated. At certain points, this serous membrane passes, in the form of folds, to the abdominal walls, and thus aids in supporting or suspending the liver. These folds constitute four of the five ligaments of the liver. The *broad, suspensory, or falciform*, ligament is a triangular double fold, attached by one border to the diaphragm, and to the anterior wall of the abdomen as far as the umbilicus, and by the other, to the upper surface of the liver, as far as the notch in its anterior margin; the remaining border is free, and extends from the notch in the liver, to the umbilicus. This latter border contains a dense fibrous cord, named the *round ligament, ligamentum teres*, fig. 96, *a*, which is formed by the remains of the umbilical vein; a structure which becomes obliterated after birth. A considerable portion of the thick posterior border of the liver, is attached, by areolar tissue, to the diaphragm, and is therefore not covered by peritoneum, which, instead, passes from one part to the other, forms the so-called *coronary ligament*, and thus helps to suspend the liver to the diaphragm. The *right and left lateral ligaments* are triangular peritoneal folds, strengthened by intermediate fibrous tissue, which pass from each side of the liver to the diaphragm.

The liver is described as consisting of five lobes. Thus, it is divided by the notch in its anterior margin, and by the line of attachment of the suspensory ligament to its upper surface, into a *right, l*, and *left lobe, l'*, the former being quadrangular in shape, and the latter somewhat triangular, and constituting

only about one-fifth of the entire organ. A deep fissure on the under surface, also marks the limit between these lobes. On its under surface, the right lobe is further divided into the following smaller lobes: viz. the *Spigelian lobe*, a pyramidal

Fig. 96.

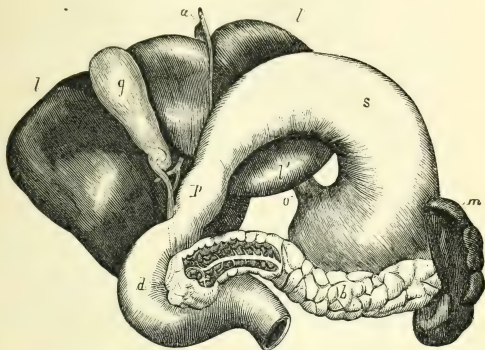


Fig. 96. View of the under surface of the liver and stomach, lifted up, to show the duodenum, pancreas, and spleen, and their mutual relations. *s*, the under or posterior surface of the stomach, which is lifted up. *o*, the oesophagus. *p*, the pylorus. *d*, the horse-shoe curve of the duodenum, or first part of the small intestine. *l*, under side of the right lobe of the liver. *l'*, *l'*, under side of the left lobe, the liver being turned up. *a*, small piece of the round and suspensory ligament of the liver. *g*, under side of the gall-bladder, ending below in the cystic duct: this is joined by the hepatic duct, formed by the union of a right and left duct, from the two lobes of the liver. The common duct, resulting from the union of the cystic and hepatic ducts, the ductus communis choledochus, or common bile duct, passes down, as shown by the dotted lines, behind the duodenum, to end with the pancreatic duct, also shown by dotted lines, by a common orifice, on a papilla, in the duodenum. *b*, the pancreas, attached to the curve of the duodenum; it is partly dissected to show its central duct, with its branches, the end of it being indicated by dotted lines, as above described. *m*, the spleen, attached to the left end of the stomach and pancreas: its anterior notched border is seen. The drawing indicates the dark colour of the spleen and liver, and the white colour of the pancreas.

mass situated near the hinder border; the *caudate* or *tailed* lobe, passing forwards from the *Spigelian* lobe; and, lastly, the *square* or *quadrate* lobe, placed between the gall-bladder and the line of demarcation between the right and left lobes.

The liver also presents, on its under surface, five *fossæ* or *fissures*, in which are contained important vessels and ducts. The *longitudinal* fissure passes, from before backwards, between the right and left lobes, and is divided into two parts; the anterior part is named the *umbilical* fissure, which contains, before birth the umbilical vein, but afterwards, the *round ligament*, the fibrous cord, left after the obliteration of that vein; the posterior part, called the *fissure of the ductus venosus*, contains, before birth, the large vein so named, and subsequently the fibrous cord remaining after its closure. Thirdly, extending nearly at right angles from the junction of the umbilical fissure with the fissure of the ductus venosus, to about the centre of the right lobe, is the *transverse* or *portal* fissure, or *porta*, the *gate*, sometimes called the *hilus* of the liver; through this the chief bloodvessels, lymphatics, nerves, and ducts of the liver pass in and out (see fig. 96). The principal vessel which enters here, is a large vein, the *vena portæ* or *portal vein*. The fourth fissure is the notch on the posterior border of the liver, which joins the fissure for the ductus venosus, and lodges the ascending vena cava and the orifices of the so-called *hepatic* veins. The fifth fissure receives the upper side of the gall-bladder.

The liver possesses three sets of bloodvessels, two conveying blood to it; viz. the *portal vein* and the *hepatic artery*, and a third set, the *hepatic veins*, which carry the blood from it. The liver in Man, and in the Vertebrata generally, is remarkable for being supplied, partly by venous, and partly by arterial, blood, for the portal vein, contrary to the usual office of a vein, conveys blood into the liver. This *portal vein*, fig. 97, *p*, is formed by the union of the veins of the abdominal organs of digestion and sanguification, excepting the liver itself, viz. by those of the stomach, *s*, small intestine, *i*, large intestine, *co*, except the lower two-thirds of the rectum, *r*, of the gall-bladder, pancreas, *d*, and spleen, *m*. The veins, from these parts, unite to form the superior mesenteric and splenic veins, which join to constitute the vena portæ. The venous trunk thus formed, *p*, is of great size, being more than half an inch in diameter. It ascends to the under surface of the liver, and entering the portal fissure, there divides into a right and left branch, for the corresponding lobes of the liver, in the substance of which it ramifies like an artery. The *hepatic artery*, which also conveys blood to the liver, is a branch of the *cæliac axis*, a short trunk given off from the abdominal

Fig. 97.

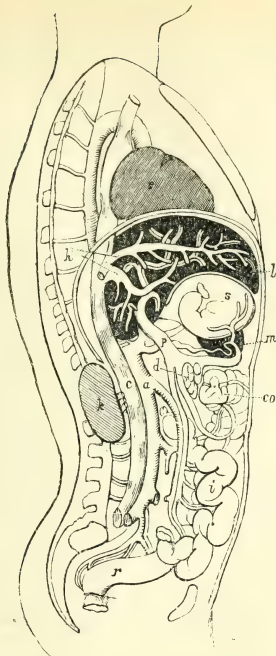


Fig. 97. Diagram to show the large vessels concerned in the so-called portal circulation. The trunk, or body, is supposed to be divided down the middle line, so as to show the cavity of the thorax or chest, above the arched diaphragm, and that of the abdomen below it. In the abdomen, *l*, is the liver; *s*, the stomach; *d*, a section of the duodenum, and pancreas; *i*, the small intestine; *co*, a part of the colon; *r*, the rectum; *m*, the lower end of the spleen; and *k*, the right kidney. The blood to all these parts, is supplied through arteries which are branches of the abdominal aorta, marked *a*. From the rectum, *r*, and the kidney, *k*, the blood is returned by veins, which end in the great ascending vein, named the ascending vena cava, marked *c*, which conveys the venous blood directly through the diaphragm, and into the right side of the heart, *o*. But the blood from the stomach, *s*; spleen, *m*; duodenum and pancreas, *d*; small intestine, *i*; and large intestine, *co* (excepting the rectum, *r*), is collected by venous branches, which end in a large venous trunk, named the vena portæ, or portal vein, *p*, by which this venous blood is conveyed to, and distributed by branches through, the liver. From this organ, it is collected by other veins, which unite to form the hepatic veins, *h*, which then join the ascending vena cava, *c*, and so reach the right side of the heart.

aorta, *a* ; it enters the liver, by the side of the vena portæ, at the portal fissure, and, like that vein, divides into a right and left branch for the corresponding lobes. The *hepatic veins*, which convey the blood from the liver, converge from all parts of the organ, to the notch in its posterior border, where they enter the ascending vena cava, by two or three main trunks, and thus the blood from the liver, mixed with that from the lower half of the body, ascends to the heart.

The liver, like all secreting glands, is provided with ducts. These, named the *hepatic ducts*, form, as they issue from the gland, two principal trunks, one from the right, the other from the left lobe. They emerge at the bottom of the portal fissure, where the two chief divisions of the portal vein and hepatic artery enter, and then unite to form a single duct named the *hepatic duct*, *ductus choledochus*, or *bile duct*. Having descended for about two inches, this joins another duct, proceeding from the gall-bladder, fig. 96, *g*, named the *cystic duct*, and so forms the *ductus communis choledochus*, or *common bile duct*. This latter duct is about three inches long, and two or three lines wide ; passing down behind the duodenum, *d*, it reaches the left or concave border of the intestine, where it comes in contact with the pancreas, and soon after, with the duct of that gland, or pancreatic duct, fig. 88, *a*, fig. 96. The two ducts then pass together, and obliquely, through the walls of the duodenum, for about three-quarters of an inch, and finally, opposite the junction of the middle and lower parts of the duodenum, about three inches below the pylorus, open upon a slight eminence of the mucous membrane, by a common and slightly constricted orifice, provided with a kind of sphincter. Sometimes, however, the biliary and pancreatic ducts open separately into the duodenum.

The lymphatics of the liver are either superficial or deep ; the former ramify upon its surface, the latter emerge at the portal fissure. The nerves are comparatively few in number ; they are derived chiefly from the sympathetic system, and, as usual with those nerves, are supported on the arteries. The pneumo-gastric nerves, especially the left, also supply a few branches to the liver. The right phrenic nerves send filaments to the peritoneal coat. Beneath the partial peritoneal investment, the liver possesses a proper *areolar* coat, which covers its whole surface, and, at the portal fissure, passes into the interior of the organ, and becomes continuous with a loose areolar tissue, named the *capsule of Glisson*, to be presently described.

The proper *substance* of the liver, is firm, and presents, on a section, a reddish-brown mottled aspect. It is composed of a multitude of compressed polyhedral masses, about the size of a pin's head, measuring from $\frac{1}{24}$ th to $\frac{1}{12}$ th of an inch in diameter, named the *hepatic lobules*; they cause the granular appearance of the torn surface of the liver. These little portions of gland substance, are held together by the ultimate ramifications of the bloodvessels and ducts, and also by a fine areolar tissue, occupying the *interlobular spaces*, and named the *interlobular* tissue, which is itself connected, on the surface of the gland, with the areolar coat. The hepatic lobules are closely arranged around certain canals, which commence at the portal fissure, branch out in all directions through the gland, becoming smaller and smaller as they proceed, and ultimately lose themselves in the interlobular spaces. These are the *portal canals*, which contain not only the branches of the portal vein, but also those of the hepatic artery, and hepatic ducts, the deep lymphatics, and the nerves. Surrounding and supporting those vessels, ducts, and nerves, is found the loose areolar tissue, named Glisson's capsule, which, outside and beyond the portal canal, is continuous with the interlobular tissue. A transverse section through a portal canal, shows a roundish space in the gland-substance, occupied chiefly by a section of a portal vein, with which, however, are associated one or two branches of the hepatic artery, and hepatic duct, the whole being embedded in the capsule of Glisson; the arteries are smaller than the duct; the canal also contains lymphatics, invisible, unless injected, and nerves supported upon the arteries; in the smallest portal canals, the parts are not so distinct. The *hepatic veins* do not lie in the portal canals, but pursue a separate course through the liver, the branches of these being seen, on a section, passing along through the gland, immediately surrounded by the lobules. As the portal veins diverge from the portal fissure, whilst the hepatic veins converge to the posterior border of the gland, their branches cross each other; moreover, they have very different relations to the hepatic lobules.

Each minute lobule has one aspect, which is named its *base*, whilst its other surfaces are called its *sides*. The *bases* of all the lobules rest upon the so-called sublobular veins, which are branches of the hepatic vein, the inner surface of which, as shown when they are opened, is marked by the polygonal outlines of the bases of the lobules. When divided trans-

versely, the lobules are polyhedral ; when cut longitudinally, they present a foliated appearance, and are seen to be supported on the sublobular hepatic veins, like sessile leaves upon a leaf-stalk.

The *sides* of the lobules are turned towards each other in the interlobular spaces, towards the portal canals, or to the surface of the liver. The portal veins, ramifying in the portal canals, give off branches which enter the interlobular spaces, and are hence named *interlobular veins*; from these, still finer branches penetrate the *sides* of the lobules, and end, within them, in the so-called *lobular venous plexus*, or *lobular capillary network*. From this network, proceeds a small vein, occupying the centre of each lobule, named the *intra-lobular vein*, and belonging to the hepatic venous system ; it opens by a minute orifice, situated in the middle of the *base* of the lobule, into the corresponding *sublobular vein*.

It will thus be seen, that the blood of the portal vein, is conveyed, by the portal interlobular veins, to the sides of the lobules, and thus reaches their internal vascular plexus, from which it is collected by the hepatic intralobular veins, and so passes out, at the bases of the lobules, into the sublobular hepatic veins, by which it is ultimately conveyed away.

From the peculiar distribution of the branches of the portal and hepatic venous systems, in each lobule, it follows that a congested state of either, influences the mottled colour of the liver in a characteristic manner. Thus when the hepatic system is congested, a rather frequent occurrence, the centre of each lobule is dark, and the circumference paler ; whilst in portal congestion, which is rare, and occurs chiefly in children, the centre of each lobule is pale, and the marginal part dark. From the great size of the portal vein, as compared with the hepatic artery, it is evident that the liver is chiefly supplied by venous blood. But even the arterial blood furnished to this organ, by the hepatic artery, appears to become venous and *portal*, before it reaches the plexus within the lobule. The hepatic artery is a nutrient vessel, supplying the framework, and not the secreting tissue, of the liver ; its branches terminate in a capillary network, in the coats of the bloodvessels and ducts, in the areolar tissue of the capsule of Glisson, the interlobular tissue, and the areolar coat of the liver ; from these parts, the blood, now become venous, is believed to be returned into the smaller portal veins, and in this *indirect* manner only, to reach the hepatic lobules. According to this

view, amongst the sources of the portal blood, must be included, not only the stomach, intestinal canal, pancreas, gall-bladder, and spleen, but also the non-secreting part of the liver itself.

The *secreting* portion of the liver is composed, in each lobule, first of the lobular capillary network or venous plexus, already mentioned, as interposed between the termination of the portal and the commencement of the hepatic venous systems; secondly, of an intermediate *gland-substance* or *parenchyma*, occupying the interstices of this capillary network; and, thirdly, of the commencements of the hepatic or biliary ducts. The gland-substance consists of roundish, or flattened, polyhedral, nucleated cells, having a delicate cell-wall, one or two bright vesicular nuclei with nucleoli, and certain faintly yellowish, semi-fluid, amorphous, granular contents, in which are commonly found larger or smaller globules of oily matter. These very peculiar cells, are named the *hepatic cells*; they vary from $\frac{1}{1030}$ th to $\frac{1}{840}$ th of an inch in diameter. They are the true secreting gland-cells of the liver, their contents closely resembling the bile, which is secreted by them. The relations of these cells to the finest commencements of the biliary ducts, and the mode of commencement of those ducts, are difficult points for investigation. The clusters of the hepatic cells occupy the interstices of the lobular venous plexus, and, whatever may be their relation to the finest commencements of the ducts, or in whatever mode the bile, formed within these cells, passes into the ducts, the hepatic cells themselves lie outside the venous plexus, and this has no direct communication with the ducts. The hepatic cells, moreover, are arranged in lines or rows, which radiate, amongst the bloodvessels, from the centre towards the circumference of the lobule. By most anatomists, these rows of cells are said to be supported on a thin basement membrane, which is continuous with the walls of the commencing efferent biliary tubes or ducts, so that the liver might be regarded as a complex gland, having ramified anastomosing ducts (Beale and Retzius). According to another view, however, the hepatic cells are merely arranged around the network of the lobular plexus, and are unsupported by a proper basement membrane (Kölliker).

The gall-bladder.—The hepatic, cystic, and common bile ducts, already described, are composed of a strong areolar coat, containing a few muscular fibres, and lined by a mucous membrane covered with a columnar epithelium; in the finest

ducts, the epithelium is squamous. The walls of these ducts present generally minute racemose mucous glands, the openings of which, are arranged in rows within the ducts. The cystic duct which leads to the gall-bladder, has, in its interior, a series of oblique crescentic projecting ridges or folds, following each other closely, so as to present the appearance of a spiral valve.

The *gall-bladder*, fig. 96, *g*, is a pear-shaped sac, from 3 to 4 inches long, about 1 inch across at its widest part, and holding rather more than one fluid ounce. It is lodged in a fossa on the under surface of the liver; its larger end or *fundus*, projects beneath the anterior border of the gland; whilst its narrow end or neck, directed, beneath that organ, upwards, backwards, and to the left, is continuous with the cystic duct. Its upper surface is attached to the liver by areolar tissue and bloodvessels; the rest is covered by the peritoneum, which therefore furnishes it with a partial serous coat. Its proper walls are composed of interlacing bands of white, fibrous, and areolar tissue, intermixed with elastic fibres, and longitudinal and circular unstriped muscular fibres. Within this areolar coat, is the mucous coat, which has a peculiar pitted or alveolar aspect, owing to the presence of innumerable fine ridges, which bound polygonal depressions of various size and form; at the bottom of the largest depressions, there are seen, by aid of a lens, the orifices of fine recesses resembling mucous follicles. The mucous membrane of the gall-bladder is usually of a deep yellow colour, and is lined by a columnar epithelium.

The gall-bladder forms a sort of receptacle, or *reservoir* for such bile as is not immediately required for the purposes of digestion. It has been shown, in animals, in which artificial openings, or fistulæ, have been made into the hepatic duct, that bile is being constantly secreted by the liver. In the intervals between the process of digestion, the secretion is slow; but, during digestion, the bile is secreted very rapidly, and at once passes along the hepatic duct, and common bile duct, into the duodenum; such bile is named *hepatic bile*. The period of most rapid secretion, in animals, has been variously stated to be from one or two hours, to ten or twelve hours after eating. According to observations made by Dalton on a dog, the quantity increases suddenly after eating, reaches its maximum in an hour, and then gradually declines; a far larger quantity enters the intestine during the first hour, than in any other

equal period. Abstinence lessens the quantity very much. In the intervals between digestion, however, the bile being secreted more scantily, has not sufficient force to pass through the narrow orifice of the common duct, and thus more or less of the secretion enters the gall-bladder; there, it undergoes inspissation, losing water, and receiving much mucus from the gall-bladder, some having been already added to it, in the ducts. It thus becomes darker, and more viscid, and, in this condition, it is called *cystic bile*. The mechanical effect of the spiral folds in the cystic duct, on the passage of the bile into, or out of, the gall-bladder, is probably to favour its entrance, and somewhat check its escape. During digestion, both cystic and hepatic bile are believed to be employed, and it is supposed that, at that period, the former is pressed out of the gall-bladder, partly by the distended stomach, and partly by the contraction of its own muscular fibres, stimulated in a reflex manner, by the acid chyme passing over the orifice of the common bile duct, the sphincter-like margin of which may be at the same time relaxed.

The analyses of bile present some discrepancies which may depend on the difference between the hepatic and the cystic bile. Speaking generally, the bile is a yellowish, or yellowish-green, viscid fluid, having a peculiar smell, and a bitter taste. In carnivorous animals, its colour is brownish-yellow; in herbivorous animals, it is generally greenish. The quantity of bile secreted by a man in twenty-four hours, is uncertain. In dogs, with artificial biliary fistulæ, the quantity secreted daily is about $\frac{1}{2}$ oz. to every pound weight of the animal, or $\frac{1}{3\frac{1}{2}}$ nd part of its weight (Kölliker, H. Müller). Supposing the weight of a man to be 140 lbs., this would give 70 ozs. or 4 lbs. 6 ozs. avoirdupois in a day, of which about $\frac{1}{2\frac{1}{3}}$ th, or nearly 3 ozs., would be solid matter. This estimate, however, appears very high. Bidder and Schmidt calculate the daily quantity secreted by man to be 56 ozs.; Nasse and Platner's observation on the dog, would give a total daily quantity for man of $33\frac{1}{2}$ ozs.; whilst others again have estimated it at only from 17 to 24 ozs. The specific gravity of the cystic bile in man, varies from 1026 to 1032; that of hepatic bile is of course less. The cystic bile of man, contains about 10 per cent. of solid matter; while the bile, from an artificial fistula in the bile duct of an animal, *i.e.* hepatic bile, contains from 3 to 5 per cent. only.

The analysis of cystic ox gall by Berzelius, gives the following percentage composition :—

Water	90.44
Bilin, with fat and colouring matters	8.	} 9.56
Mucus, chiefly cystic3	
Salts	1.26	
								<hr/> 100.00

The analyses by other chemists, show a similar composition, but, according to Strecker, the *bilin* of Berzelius is a compound substance. Its two characteristic constituents are the colourless conjugated fatty acids, named *glycocholic* or *cholic*, and *taurocholic*; the one formed by the combination of a nitrogenous body, named *glycocin*, or *glycocoll*, and *cholalic* acid; the other, formed by the union of the same acid with another nitrogenous body, which contains sulphur, named *taurin*. The chemical relations of these substances may be seen, by comparing their atomic compositions (Vol. I., p. 98).

Cholalic acid crystallises in white tetrahedra; dissolved in sulphuric acid, with the addition of sugar, it yields a purple violet colour, the reaction of the so-called Pettenkofer's test for bile. Glycocoll, obtainable also by the action of acids or alkalis upon glue and some other animal substances, forms hard, transparent, colourless, crystals, soluble in water, but nearly insoluble in alcohol and ether. Taurin crystallises in white hexagonal prisms, inodorous and almost tasteless; it contains the large proportion of one-fourth its weight of sulphur; it leaves much sulphurous acid on being burnt, and gives off sulphuretted hydrogen when decomposed. Both glycocoll and taurin are neutral substances, having a tendency to unite with acids, to form, as in the bile, conjugated acids. Glycocholic, or cholic acid, consists of fine crystalline needles, soluble in water and alcohol, but very slightly so in ether, having a bitter sweet taste, and a strong acid reaction. Taurocholic acid has not yet been obtained in a crystalline form. In the bile, the glycocholic and taurocholic acids, which form from 4 to 7 per cent. of that secretion, are always united with soda, as glycocholate and taurocholate of soda. The bile, however, occasionally contains an excess of some base; for, though often neutral, it may be feebly alkaline. The substance of the liver has, or rapidly acquires after death, an acid reaction. The proportions of glycocholic and taurocholic acids, vary in the bile of different animals, but are tolerably constant in each species. In the dog, the glycocholic acid is scanty, and sometimes

absent. In the pig, another allied acid is found, named *tyrocholic*, and a small quantity of an acid analogous to the *aurocholic*. In the goose, a different allied acid exists, named *auro-chenolic*. Although varied in different animals, and present in variable proportions, the characteristic constituent of the bile is, in all cases, a soda salt of some fatty acid, resembling the acids of fatty and resinous bodies. The sulphuretted and nitrogenous body, *taurin*, is always present.

The next most characteristic constituent of the bile, is its colouring matter, named by different chemists, *cholepyrrhin*, *bilipyrrhin*, and *biliphæin*. This forms about 5 per cent. of the secretion. According to Berzelius, two modifications of colouring matter exist in bile. The one, a *yellowish* colouring substance, was named by him *bilifulvin*; it seems to coincide with the *cholepyrrhin* and *biliphæin* of other writers. It is uncrystallisable, insoluble in water, only slightly soluble or insoluble (Brücke) in alcohol, but especially so in caustic alkalies, and in chloroform. It affords a peculiar reaction with nitric acid or nitrates, which, when added in small quantities to the yellow alkaline solution, first produce a green colour, then blue, violet, and red, and finally yellow again, owing, it is supposed, to the occurrence of different degrees of oxidation. The other colouring matter of the bile, smaller in quantity, is *green*, and hence was named by Berzelius, *biliverdin*; it was supposed by him, though not proved so, to be identical with chlorophyll. It is insoluble in chloroform, slightly so in alcohol, and insoluble in water; it appears to be a more highly oxidised form of *bilifulvin*. These colouring matters are closely allied to the *hæmatin*, or *cruorin* of the blood; but neither these, nor the fatty acids of the bile, pre-exist in the blood; they are formed in the liver by the hepatic cells.

In addition to these, its essential constituents, bile contains about 1 per cent. of ordinary fats, *margarin* and *olein*, or alkaline margarates and oleates. It also presents traces of *cholesterin*, the fatty or resinoid body, which likewise exists in nervous substance, in the blood, and in certain diseased exudations. *Cholesterin* crystallises in brilliant colourless plates, insoluble in water, soluble in boiling alcohol and in ether, and absolutely resisting saponification. In the living body, it is probably held in solution by fluid fats. The bile contains about 1 per cent. of salts, its ashes yielding, besides soda in large proportion, traces of potash, magnesia, and lime, in combination with phosphoric acid and chlorine. The

mucus found in bile, indicated by the presence of mucous and epithelial cells, is an adventitious substance, derived from the walls and follicles of the bile ducts or gall-bladder.

Besides being engaged in the formation of biliary substances, partly intended for use in the digestive process, and partly destined, as we shall hereafter explain, to be thrown out of the body as excrementitious matters, the liver has recently been discovered to perform another most remarkable office in the economy, viz. that of separating from the blood by its cells, a substance named *glycogen*, or *animal starch*, which has the property of being rapidly transformed into glucose, or grape sugar. This sugar is supposed to enter the hepatic blood, to proceed with it to the heart, and thence to the lungs, to be oxidised in the respiratory process, and aid in the development of heat. This *glycogenic* or *sugar-forming* function of the liver, will be more fully noticed in the section on Secretion.

Sources and Composition of the Pancreatic Juice.

The *pancreas* (πᾶν κρέας, all flesh), or abdominal sweetbread, is a long, narrow, pinkish, gland, flattened before and behind, having its right, larger end lodged in the concavity of the duodenum; whilst its left, pointed extremity, touches the spleen. Its shape has been compared to that of a dog's tongue, or of a hammer. It crosses over the front of the first lumbar vertebra, behind the lower border of the stomach, and is held in place by its attachment to the duodenum, by its bloodvessels, nerves, lymphatics, and ducts, by areolar tissue, connecting it with adjacent parts, and by a peritoneal layer. It is about 6 or 8 inches long, $1\frac{1}{2}$ inch broad, and from $\frac{1}{2}$ an inch to 1 inch thick, being thicker at its larger end. It usually weighs between $2\frac{1}{4}$ and $3\frac{1}{2}$ ozs, but sometimes as much as 6 ozs.

In structure, the pancreas resembles the salivary glands, and has been termed the *abdominal* salivary gland. Its numerous lobes and lobules are compressed, and are held together by the vessels, ducts, and interlobular areolar tissue. Each lobule, like those of the parotid gland, fig. 42, *c*, consists of a branched duct, ending in rounded vesicles, surrounded by networks of capillaries. The ducts from the numerous lobes, join a principal duct, which runs through the gland from left to right. This duct, the *pancreatic duct*, or *canal of Wirsung*, who discovered it in the human body, in 1642, is

about the size of a small quill; it emerges from the larger end of the gland, and, accompanied by the common bile duct, passes, with it, obliquely through the walls of the duodenum, and, about 3 inches below the pylorus, opens into the intestine by a common orifice with the bile duct, or sometimes by a separate aperture. Occasionally there exists a supplementary pancreatic duct, which enters the duodenum about an inch from the chief duct.

The secretion from the pancreas, or the *pancreatic juice*, is a somewhat viscid, transparent, colourless, and inodorous fluid. The quantity secreted daily, in animals, varies, according to different observers, from 15 to 35 grains per hour for each pound weight of the body; so that in a man weighing 140 pounds, the quantity secreted would be from $4\frac{3}{4}$ ozs. to 11 ozs. per hour. The secretion is probably not continuous, and its quantity increases as digestion goes on, the activity of the process being, by some, referred to the absorption of albuminoid substances already digested. From these fluctuations, it is impossible to estimate correctly the quantity formed daily; which has been differently estimated at from 7 ozs. to $16\frac{1}{2}$ lbs. Statements, almost as discrepant, have been made concerning the gastric juice and bile, correct results, as regards these internal secretions, not being so attainable as in the case of the saliva. The collection of these fluids, by aid of artificial fistulæ, in animals, is open to the objection, that the conditions, especially of the nerves, which govern the quantity of the secretion, are not healthy. The total quantity of the digestive fluids poured into the alimentary canal, after taking food, is, however, much greater than was formerly supposed, and, in comparison with the blood circulating in the body, is very great.

The solid constituents of the pancreatic juice, as estimated from cases of artificial fistulæ in animals, vary from 1.5 to 6, or even 10 per cent.; the more rapid the secretion, the less solid matter it contains. Its most peculiar constituent is an albuminoid substance named *pancreatin*, the special composition of which is not yet determined. Like salivin, this substance is soluble in water, coagulable by heat, and precipitable by alcohol, but may again be dissolved in water; unlike albumen, it is precipitated by sulphate of magnesia. To the pancreatin, are attributed the peculiar digestive properties of the pancreatic juice, which differ, in one respect most remarkably, from those of the saliva. The pancreas, indeed, resembles

the salivary glands anatomically, but not physiologically; for its secretion is much more viscid, is coagulated by strong mineral acids, and does not contain sulpho-cyanide of potassium. Its salts, about $\cdot 5$ to 1 per cent., are chiefly chloride of sodium and phosphate of lime and magnesia. Like the saliva, it is alkaline, but more strongly so; as digestion proceeds, it becomes more alkaline, but less viscid and coagulable. On standing, it speedily becomes neutral and then acid; it soon putrefies, but may be preserved for a few days, at a temperature of 45° ; its properties are destroyed by a heat slightly above that of the body. It contains the débris of a few nucleated cells.

Sources and Composition of the Intestinal Juices.

The mucous membrane of the small intestine, is provided with two kinds of secreting glands, named respectively, after their discoverers, the *glands of Brunner* and the *glands, follicles, or crypts of Lieberkühn*. The secreted products of all these glands, constitute the *succus entericus*.

Brunner's glands are found in the duodenum, being most abundant near the pylorus, and disappearing lower down, very few being present at the commencement of the jejunum. They are compound racemose glands, like the buccal and labial glands, and appear to bear the same relation to the pancreas as those glands do to the salivary glands. They secrete a viscid alkaline mucus.

The *follicles* or *crypts* of *Lieberkühn* are found throughout the small and large intestines. They consist of multitudes of minute tubuli, closed at their deep extremities, but opening on to the surface of the mucous membrane, perpendicularly to which they are arranged, more or less closely together. In the small intestine, they measure from $\frac{1}{80}$ th to $\frac{1}{60}$ th of an inch in length, and about $\frac{1}{400}$ th of an inch in diameter. Their orifices are seen, fig. 98, by aid of a lens, in all parts of the small intestine, even on the valvulæ conniventes, between the villi, and also in little circlets, around the closed sacs of the so-called agminated glands. Their total number has been estimated at several millions. They are sometimes flask-shaped, but never subdivided, like the gastric glands; they are lined with a columnar epithelium, fig. 99, and are surrounded by capillaries.

They contain a transparent granular fluid, the *intestinal*

juice proper; sometimes they are distended with opaque mucus, and desquamated epithelial cells destitute of fat. The composition of the intestinal juice, is not well known; it probably differs from ordinary mucus, and has special properties; it is colourless and viscid, and is usually described as being strongly alkaline, but, according to others, it is acid in a great part of the small intestine; it contains from 2 to 3.5 per cent. of solid matter, in which is included an organic substance, precipitable by alcohol and resolvable in water, but forming insoluble precipitates with metallic salts.

Attempts have been made to collect it, from animals, by ligaturing previously emptied portions of intestine, or by forming

Fig. 98.

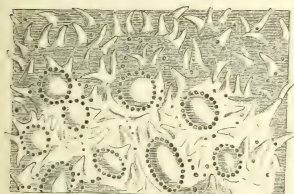


Fig. 99.

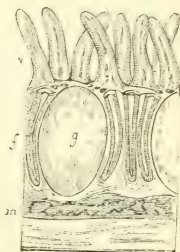


Fig. 98. Portion of the border of a Peyer's patch, magnified about twelve diameters. It shows the minute pointed processes named the villi of the small intestine, found both on the general surface, and also on the lighter part or Peyer's patch. On this latter, are seen the rounded or oval sacs, constituting the agminated glands, with the villi between, not upon, them. Around the borders of these, are circlets of the orifices of the intestinal tubuli, or crypts of Lieberkühn, others of which are seen, scattered over the general surface between the villi. (After Boehm.)

Fig. 99. Diagrammatic vertical section of one sac, and a part of another, from a patch of Peyer, with the surrounding parts. *g*, the sac with its granular contents. *f*, one of the intestinal tubuli, crypts, or follicles of Lieberkühn, of which three others are seen, on the other side of the sac. *v*, the intestinal villi, on the surface of the mucous membrane, covering the patch. *m*, cut ends of the circular muscular fibres; beneath these, the longitudinal fibres, and the serous or peritoneal covering of the intestine. (After Kölliker.) Magnified forty diameters.

artificial intestinal fistulæ; but the fluid so obtained, must differ from the normal secretion. The quantity daily secreted in Man is uncertain, but is doubtless considerable, especially after meals.

The tubuli or crypts of Lieberkühn of the large intestine, are longer, wider, more numerous, and more closely arranged than those of the small intestine. The entire surface presents, when examined with a lens, a cribriform aspect, due to the numerous orifices, which, in the lower part of the intestine, are almost visible to the naked eye; they are lined with columnar epithelium. Besides these crypts, there are found, scattered over the mucous membrane of the large intestine, small *depressions*, resembling saccular glands; they were formerly described as *solitary glands*, but they are lined with a columnar epithelium only, and are placed over certain closed sacs, exactly similar to those of the so-called solitary glands of the stomach and small intestine, and of the agminated glands of the latter.

The intestinal juice of the large intestine, resembles, so far as is known, that of the small intestine, being composed partly of mucus, but chiefly of a special secretion, which is said to be alkaline, though, in the cæcum, the intestinal contents are acid.

CHEMICAL PROCESSES OF DIGESTION. ACTION OF THE DIGESTIVE FLUIDS, WITH HEAT.

As already stated, the purpose of the digestive process in the animal economy, is the reduction of alimentary substances into a soluble and absorbable condition, a state of solution, or of exceedingly minute subdivision and suspension in a fluid, being an essential condition, antecedent to the absorption of any nutrient substance into the living tissues. Food, as we have seen, considered chemically, consists of water, alkaline and earthy salts, and certain important organic proximate constituents, which are classified into non-nitrogenous and nitrogenous substances.

Of these, the water, the natural medium of solution or suspension of the solid alimentary substances, and likewise the saline substances, both alkaline and earthy, which are mostly dissolved in it, correspond with the water which forms three-fourths of the soft tissues of the body, and with the water and salts of the blood: they are directly absorbed without any digestive change. The organic constituents, whether non-nitrogenous or nitrogenous, are some of them soluble, and some insoluble in water at the temperature of the interior of the body, viz. about 102°. The *soluble* non-nitrogenous bodies

are pectin, gum, dextrin, sugars, alcohol, organic acids, and ethers. The soluble nitrogenous substances are certain forms of albumen, fibrin, casein, gelatin, and chondrin; the albuminoid principles of the digestive fluids, viz. salivin, pepsin and pancreatin, which are probably in a state of solution in the living body; creatin and creatinin; cerebriacid; and thein, caffen and theobromin. Many of these also are possibly directly absorbed. The *insoluble* organic constituents are the non-nitrogenous cellulose, starch, and fatty matters; and the nitrogenous solid forms of albumen, syntonin, casein, fibrin, gluten and legumin, and the gelatin and chondrin-yielding tissues. All these, however soft or minutely divided, must be dissolved, before they can be absorbed. They are the most abundant constituents of our food: in all kinds of bread, and biscuit, in cooked potatoes, rice, sago or tapioca, the quantity of insoluble starch is greater than that of soluble starch, gum, dextrin, or sugar; in cooked meat, poultry, fish, and eggs, and also in cheese, the albuminoid constituents are all solidified; the vegetable gluten and legumin are either solid, or are coagulated by cooking; and even the fluid or finely granular casein of milk, is first precipitated or curdled in the stomach, by the action of the acid gastric juice. Indeed, undissolved, though minute, granules of amyloid, insoluble oleoid, and solidified albuminoid substances, constitute the most nutritive forms of food.

In a chemical sense, these substances are instable compounds; they have a high atomic constitution, and are easily broken up by powerful chemical agents, by elevated temperatures, fermentation, or putrefaction. Nevertheless, under ordinary circumstances, they are insoluble in water at the heat of the body, and are decomposable, or rendered soluble, only by the action of agents and temperatures, which would be destructive to living animal tissues. Thus, starch is rendered mucilaginous only at the temperature of 160° ; it is changed into dextrin at a still more elevated temperature; and it is convertible into a sugar, by the highly corrosive sulphuric acid. Of the fats, margarin and stearin become fluid only at temperatures higher than that of the body, viz. 114° , and 118° ; none of them are easily miscible with, or can be kept suspended, in minute particles, in watery fluids; and to render any of these soluble in water, they must be saponified by the action of caustic alkalies, which are destructive to living tissues. The solid albuminoid principles, so far from being soluble even in boiling water, have their component particles knit still more firmly together, by

being boiled; and putrefaction alone will dissolve them,—a condition inconsistent with their retention of nutritive properties, and, indeed, converting them into noxious products.

The *first* problem of digestion, however, is to render such substances, which, in this point of view, are *refractory*, soluble at a temperature, and by means of agents, compatible with the life and integrity of the digestive organs themselves. But, *secondly*, starch, even when dissolved, so as to form a soluble mucilage, and also albumen, when perfectly soluble as in the white of egg, are too tenacious to pass readily through moist membranes, and belong to the so-called *colloid* bodies, which have a feeble permeating power, in comparison with the so-called *crystalloid* substances (Graham); whilst oil, likewise, passes through moist membranes, only under considerable pressure. Accordingly, in the process of digestion, starch is not only dissolved, but is converted into the crystalloid, and highly permeating substance, *sugar*; albuminoid bodies are converted into a substance named *albuminose*, which, though not shown to be crystallisable, nevertheless, permeates moist membranes with great facility; whilst fatty matters are either emulsified, decomposed, or dissolved. These transmutations are daily accomplished, within the body, at its *proper temperature*, in modes at present only hypothetically explained, by the respective actions of the salivin, pepsin, pancreatin, and conjugated fatty acids, of the saliva, gastric juice, pancreas, and bile.

Action of the Saliva and other Fluids of the Mouth.

The saliva, the chief fluid poured into the mouth, acts first, by its watery basis, as a solvent, contributing thus also, to the perfection of the sense of taste. It dissolves saline substances, the organic acids, alcohols, and ethers, gum, sugar, and the soluble albuminoid and gelatinoid bodies. Secondly, and most importantly, the saliva changes the starch granules, first into dextrin, and then into soluble and crystalloid dextrose, glucose or grape-sugar, ready for absorption. Dextrin has the same atomic constitution as starch, $C_6H_{10}O_5$, whilst grape sugar, $C_6H_{12}O_6$, appears to be produced from it, by the taking up of 1 atom of water H_2O . No evolution of gas takes place, as occurs in alcoholic fermentation. The change is more rapid than fermentation. On adding some saliva to a weak solution of boiled starch, and immediately testing it with iodine, the blue colour of

iodide of starch fails to appear; or, on mixing saliva with a small quantity of cooked starch, already rendered blue by iodine, the colour is discharged. (Vintschgau.) These facts prove that the starch is changed; its conversion into sugar, is shown by examination with a polariscope, or by boiling the fluid, after adding a slightly alkaline solution of tartrate of copper, when a yellowish red precipitate of oxide of copper is thrown down, indicating the presence of grape-sugar (Trommer's test).

The parotid saliva is, by itself, able to convert starch into sugar; that of the submaxillary and sublingual glands accomplishes the change, when combined with the mucus of the mouth, which, indeed, has, by some, been regarded as the sole agent in this transformation. A mixture of all the fluids of the mouth appears, however, to form the most active combination for this purpose. Besides the saliva and buccal fluids, the pancreatic juice possesses this property in great perfection; but the gastric juice and the bile do not. Most animal membranes also, such as the mucous membrane of the mouth, intestines, and even the bladder, particularly if they are in a state of commencing decomposition, exhibit this power.

The constituent of the saliva, to which this peculiar power of transmutation is due, is the *salivin* or *ptyalin*, which is said to act catalytically, or by *presence*, or contact; for if this albuminoid substance be precipitated by alcohol, collected on a filter, and re-dissolved in water, it will still effect the transformation very rapidly, and will convert 2,000 times its own weight of starch into sugar. Neither dilute *alcohol* or *acids*, nor, it is said, even a boiling heat, arrest altogether the action of salivin. Finally, although the action of saliva is more rapid and complete on cooked starch, yet grains of raw starch, masticated and mixed with saliva in the mouth, and then maintained at a temperature of 100°, at length break down, and are converted into sugar. The saliva has no specific action on gum, pectin, cellulose or fatty matters, unless it may, to a slight degree, emulsify the latter, nor yet on albuminoid or gelatinoid substances.

Action of the Gastric Juice, and Mucus of the Stomach.

It is the gastric juice, secreted by the peptic glands, which accomplishes the act of gastric digestion; the secretion of the racemose glands, lined with columnar epithelium, found near the pyloric end of the stomach, is supposed not to participate

in this office, but it may act in the further conversion of starch into sugar. In this stage of digestion, albuminoid and gelatinoid substances are specially acted upon, and are reduced to a pulpy mixture, containing the so-called *albuminose* or *peptone*. The solid or insoluble forms, such as coagulated albumen, syntonin, and fibrin, are slowly dissolved; certain of the soluble forms, as the casein in milk, and the albumen in vegetable juices, are first precipitated, and then dissolved; whereas fluid albumen, as the raw white of egg, remains in solution whilst it is being converted into albuminose. Albuminose resembles the albuminoid bodies in chemical composition, though differences will probably hereafter be detected in it. Whatever the peculiarity of the albuminoid body, whether it be albumen, syntonin, fibrin, or casein, gluten or legumin, it is transformed into an almost identical albuminose. Moreover, this albuminose, or peptone, possesses properties which distinguish it from the albuminoids. Thus, it is no longer coagulable by heat, nor by the action of nitric acid, though still precipitable by tannic acid, metallic salts, and strong alcohol; it is soluble in all proportions in water, so much so, that the act of digestion of the albuminoids, or their conversion into albuminose, has been referred hypothetically to a kind of hydration of the albuminoids, or a taking up by them, of certain atoms of water, just as the hydration of starch or dextrin, appears to be a step in their conversion into sugar. Gelatin, and the gelatin-yielding tissues, furnish a special kind of peptone, a viscid fluid, which does not, according to some, gelatinize or stiffen in the cold. The transformation of albuminoid and gelatinoid substances into the ultimate albumen and gelatin-peptones, is not sudden, but is characterised by intermediate stages, in which less soluble forms of these substances appear, named *parapeptones*. Parapeptone is precipitated, in the form of flocculi, from the peptone, when their mixed acid solution is neutralised by an alkali; it is insoluble in water, though gradually dissolved by weak acid and alkaline solutions. The peptone, as already said, is highly soluble in water, and precipitable by tannic acid, alcohol, and metallic salts. When a solution of peptone is injected into the blood of an animal, it does not appear in the renal excretion; but when albumen, dissolved in very weak hydrochloric acid, is employed in a similar manner, albumen is found in the urine. These facts indicate that a true metamorphosis is effected in the albuminoid constituents

of food. The peptone ultimately produced, is not only freely soluble in water, but most readily permeates moist animal membranes, and hence is a substance admirably fitted for absorption.

The gastric juice has no peptic action upon either the amyaceous or oleaginous constituents of food.

The agent by which the gastric juice dissolves, or excites the solution of, albuminoid and gelatinoid substances, is the peculiar animal substance, itself albuminoid, the *pepsin*; but the free acid contained in it, is also essential to the digestive process. Dilute hydrochloric, or other acid, of the strength of that present in the gastric juice, possesses by itself no digestive property, though it renders the tissues semi-transparent, and dissolves out earthy matter from bones. Again, pepsin alone, obtained pure by precipitation from the gastric juice by means of alcohol, filtration, and re-solution in water, also possesses no digestive power; nor does pure gastric juice, provided that its acid be carefully neutralised; for small pieces of meat, or albumen, placed in such solutions, do not digest, but after a time putrefy.

These, and many other, facts concerning the rapidity and results of digestion, have been established by experiments, amongst the most interesting in Physiology, on *artificial digestion*, i.e., by subjecting different substances to the action of different digestive fluids, under exactly like conditions. The temperature employed may vary from 96° to 102°. During natural digestion, the temperature of the stomach of Alexis St. Martin, was found to be from 100° to 101° F.; whilst during fasting, it was 98° or 99°. (Dr. F. Smith.)

An artificial digestive fluid may be obtained directly from the human or animal stomach, by first exciting the flow of gastric juice, and then causing vomiting; or it may be collected from artificial gastric fistulæ in animals. A digestive fluid may, however, be more conveniently, and less cruelly, obtained from the gastric mucous membrane of the recently killed sheep, calf, ox, or pig, especially if the animal be slaughtered whilst digestion is going on in the stomach. Finely cut portions, or scrapings, of the mucous membrane, are to be macerated in 20 times their weight of *cold* water for 24 hours, with frequent agitation of the mixture. A temperature as low as 50° is desirable, to prevent the pepsin, extracted from the membrane, from exhausting itself, more or less, in the digestion of that membrane itself. The fragments of the mu-

cous membrane being allowed to subside, the supernatant fluid is poured off, forming a solution of pepsin extracted from the peptic cells, but containing only a slight and insufficient quantity of free acid; for the pepsin is stored up in the peptic cells, so that it may be extracted by water after death, whilst the acid of the gastric juice is probably secreted only when required, perhaps by the columnar epithelial cells; it therefore ceases on the death of the animal. Hence the solution of pepsin as above prepared, requires an addition of hydrochloric acid, to make it digest actively. Too little, or too much, acid diminishes its peptic properties. Ten minims, *i.e.* about 13 drops of the pure hydrochloric acid of commerce, to every ounce of the digestive fluid, is said to be the best proportion.

The inefficiency of the acid, and of the solution of pepsin, separately employed, and the powerful effect of the two together, may be thus strikingly illustrated. Three fluids are to be prepared, one, of hydrochloric acid and water, in the proportion of 13 drops to the ounce; a second, of the above described solution of pepsin, exactly neutralised by carbonate of soda; and a third, of the same solution, acidified with hydrochloric acid, in the proper proportions. In equal quantities of these fluids, contained in glass jars of the same size, are suspended the legs of fowls, or the fore-limbs of rabbits, either cooked or uncooked, one in each jar; the jars are then placed in a water-bath, and maintained at a temperature ranging between 96° and 102° , for 24 hours. At the end of that period, the limb suspended in the hydrochloric acid and water, is found to be slightly swollen, pale and semi-transparent, whilst the solution, itself of a yellowish tint, is quite clear, and free from deposit. The limb submitted to the action of the neutralized solution of pepsin, which is itself slightly turbid, appears sodden, but its surface is nowhere dissolved; the fluid itself is darker, but not more turbid. In the acid solution of pepsin, however, all the soft parts of the digested limb are, *as it were, eaten away and pulpified*, or dissolved; the tendons disappear first, then the muscles, next the ligaments, and lastly, even the bones and cartilages are more or less attacked, the slight residual mass contrasting strongly with the undissolved and swollen limbs in the other two solutions; moreover, the fluid itself has a brownish colour, and presents a soft flocculent or pulpy grumous sediment, several inches deep, which, on the slightest agitation, mixes easily with the fluid above, and resembles the digested contents of the stomach, after taking animal food.

Phosphoric, sulphuric, and even nitric acid may be employed in the artificial digestive fluid, but they are not so suitable as hydrochloric. Very strong acids, metallic salts, caustic alkalies, alum, tannin, and strong alcohol, destroy its digestive properties, and so does a temperature of 120° . A strongly acid artificial gastric juice is better suited for the digestion of some substances, such as coagulated albumen, the solid syntonin of cooked muscle, and legumin; whilst fibrin is more quickly dissolved in a feebly acid juice, even 1 drop to 1 oz. of fluid. (Brücke.) The strongly acid natural gastric juice of the Carnivora, acts most quickly on the firmer animal albumen, but the less acid secretion of the Herbivora, most quickly on the softer vegetable gluten. The human gastric juice has a feebler power even than that of the herbivora; its acidity declares itself immediately on the introduction of food into the stomach, and increases, for a time, as digestion goes on, when the less digestible food requires to be attacked; when the stomach is empty, the acidity quite disappears.

The power of the gastric juice to dissolve animal substances, is well illustrated by the softening or digestion of the coats of the stomach by its own secretion, after death, often noticed both in men and animals dying whilst digestion is going on: all the coats of the stomach may be thus perforated; in the human body, the effects may simulate the action of a corrosive poison.

The immunity of the living gastric mucous membrane, or its power of resisting the solvent action of its own secretion, has been variously explained. According to one view, the epithelium and mucus constitute a sufficient protection; for when the former is detached, the subjacent tissue is said to be attacked, in the living stomach, as well as after death. The 'vitality' of the mucous membrane (the sum of its vital actions), has been supposed to enable it to resist solution; and this resistance necessarily ceases on the death of the part. A more recent view, founded on many experiments, attributes the non-solution of the living mucous membrane, to the protecting influence of the blood in the capillaries, which is supposed to maintain, so long as the circulation continues, the alkalinity of the tissues, a chemical condition incompatible, as we have seen, with peptic digestion. (Pavy.)

The digestive action of the fluids of the living stomach was shown long ago by Spallanzani, Stevens, Tiedemann, Gmelin, and others, who induced dogs to swallow pieces of sponge

fastened to strings, and afterwards withdrawing them, obtained a quantity of fresh gastric juice, which slowly dissolved food, kept in it at a temperature of 100°. But the most direct evidence of the solvent power of gastric juice, is that obtained by Dr. Beaumont, who employed the fluid collected from the stomach of the Canadian voyageur, Alexis St. Martin. With that fluid, the process of solution was very rapid. Three drachms of boiled beef placed in an ounce of fluid, maintained at a temperature of 100°, began to digest in 40 minutes; in 60 minutes, a pulpy deposit began to form; in 2 hours, the areolar tissue was digested, leaving the muscular fibres disconnected or loosened; in 6 hours, these were nearly all digested; and in 10 hours, the meat was completely dissolved; the gastric juice, from being transparent, was now the colour of whey, and contained a meat-coloured sediment. Digestion was still more rapidly accomplished, when a similar piece of beef, attached to a thread, was placed in Alexis St. Martin's stomach; for, although at the end of one hour, its condition appeared much the same as that of the piece of beef digested in the gastric fluid out of the body, at the expiration of two hours, it was completely dissolved.

From these and other experiments, it is evident, that, with the exception of the rapidity of the two processes, artificial and natural digestion are identical in character. The rapidity of natural, as compared with artificial digestion, may probably be explained, partly by the more powerful action of a continuously fresh supply of gastric juice, and partly by the constant removal of the outer pulpified layer of the nutrient mass, by the incessant pressure and motion of this mass by means of the muscular coats of the stomach. Artificial digestion is much accelerated by occasional agitation.

The mere quantity of fluid employed in natural digestion, must also be very important. It has been shown, from experiments on the gastric juice of the dog, that 20 ozs. of fluid are needed for the digestion of 1 oz. of albumen. The daily quantity of gastric juice secreted by a man, 140 lbs. in weight, has been estimated at 14 lbs. or 11 pints imperial. A pint of saliva, which is a moderate estimate, and 2 pints of water consumed as beverage, would make a total of 14 pints of fluid, employed in the gastric digestion of the daily solid food; beyond the stomach, $2\frac{1}{2}$ pints of bile, $1\frac{1}{2}$ pint of pancreatic juice, and one pint of intestinal juice are added. The total quantity of fluid employed in the digestive

process in 24 hours, certainly exceeds the quantity of blood in the body, which, taken at $\frac{1}{13}$ th part of the weight of the latter, would be, for a Man weighing 140 lbs., less than 11 lbs., or 9 pints. It is evident, therefore, that the large quantities of fluid, daily secreted for the purposes of digestion, can only be supplied by a circular movement of the same aqueous particles, in successive acts of secretion, absorption, re-secretion, and re-absorption. The water which leaves the blood, to form part of the digestive juices, re-enters the blood with the absorbed food, once more leaves it in the newly formed digestive juices, and is again re-absorbed, until digestion is complete. This continued irrigation of the food, combined with the activity of the freshly formed gastric juice, must greatly contribute to the rapidity of natural digestion.

That the pepsin of the gastric juice, is the special agent in the gastric digestion of albuminoid and gelatinoid substances, is easily shown. By evaporating the natural gastric juice, or the artificial solution of pepsin, to a viscid consistence, and adding strong alcohol to it, the pepsin is precipitated in whitish flocculi, which may then be separated by filtration, from the other constituents of the gastric juice, dried at a low temperature, and preserved for months. The dried pepsin thus obtained, forms a firm, greyish, mass, or powder; it is easily soluble in, or miscible with, water, and 1 grain dissolved in so large a quantity as 60,000 grains, i. e. $6\frac{1}{4}$ pints of acidified water, still possesses digestive properties. Pepsin, whether dry or dissolved, as in natural or artificial gastric juice, loses its digestive power, if it be subjected to a temperature a little above that of the body, for example, a heat even of 120° . It is likewise rendered inactive, by strong chemical reagents. It is remarkable that alcohol, which precipitates it, and temporarily suspends its digestive properties, does not destroy them; for on sufficient dilution with water, it is redissolved, and again becomes active. The energy of pepsin, like that of salivin, in converting starch into sugar, is catalytic. The action of contact or pressure, exhibited by both these substances, differs from that of the yeast ferment in the alcoholic fermentations, in not causing the evolution of any gas, and in not being continually reproduced. It is said, however, by some, that the pepsin does not itself undergo waste in the process of digestion; but the power of a given quantity is certainly limited. Salivin and pepsin have been regarded as albuminoid bodies in *a state of change*, and capable of

inducing changes in other albuminoids, with which they are brought into contact. Putrescent albuminoid substances, as is well known, can propagate putrescent changes to fresh albuminoid substances, and can also convert starch into sugar, or one form of sugar into another. But pepsin is not a putrescent body, nor is the peptone, produced by its action on albumen, putrefied. On the contrary, it has been shown by experiment, that fresh gastric juice, applied to putrid meat, first arrests putrefaction, removing its signs, and then digests the meat. Like fermentation and putrefaction, however, digestion is retarded by low temperatures, altogether arrested at a temperature of 34° , and is stopped by high temperatures, by the action of absolute alcohol, strong acids, alkalies, and metallic salts.

The action of the gastric juice varies, according to the character of the food, its state of comminution or subdivision, and its condition of dryness or moisture. In order to determine the time required for the solution of different nutritive substances, these have been introduced, inclosed in perforated tubes of metal or glass, into the stomachs of animals, and then have been withdrawn; or, animals have been fed with such substances, and afterwards killed at certain intervals. The most important observations, however, are those made by Dr. Beaumont in the human subject. In the stomach of Alexis St. Martin, a mixed meal of animal and vegetable food, was nearly all dissolved into a pulp, within an hour; and the stomach was completely emptied in $2\frac{1}{2}$ hours. A breakfast, consisting of three hard boiled eggs, some pancakes with coffee, being taken at 8 o'clock, the stomach was empty at 10.15. Two roasted eggs and three apples, eaten at 11 o'clock on the same day, had disappeared at 12.15. Roast pig and vegetables, afterwards eaten at 2 P.M., were half dissolved at 3, and had disappeared at 4.30. It was further observed, that a meal, consisting of boiled dried cod-fish, potatoes, parsnips, bread and butter, eaten at 3 o'clock, was about half digested at 3.30, the bread and parsnips having disappeared, the fish being separated into threads, and the potatoes being least altered; at 4 o'clock, very few pieces of the fibre of the fish were found, but some of the potato was still perceptible; at 4.30 all was completely pulpified; and at 5 o'clock, the stomach was empty. Again it was found, that rice and tripe were digested in 1 hour; that eggs, salmon, trout, apples, and venison, took $1\frac{1}{2}$ hour; tapioca, barley, milk, liver, and fish,

2 hours; turkey, lamb, potatoes, pork, $2\frac{1}{2}$ hours; beef, mutton, and poultry, from 3 to $3\frac{1}{2}$ hours; and veal a little longer. The order in which each separate article of food is mentioned above, indicates its relative digestibility, at least in the stomach of Alexis St. Martin.

As a rule, animal substances are more rapidly digested than vegetable substances. The rate of digestion of different substances corresponds with the relative necessity for their being acted on by the gastric juice. Thus, those which require the most digestion by that fluid, necessarily remain the longest, whilst those which are merely liberated, but are not dissolved in it, pass out sooner; and fluids, with their soluble ingredients, disappear the most quickly. In cases of fistulous openings in the dog, and in Man, it has been found that fibrin is digested in half an hour, casein in $1\frac{1}{2}$ hour, gelatin in 2 hours, coagulated albumen in 6 hours, and tendons in 10 hours.

During gastric digestion, the muscular tissue breaks up first into its fasciculi, and then into fibres, the striæ of which gradually disappear, the sarcolemma, as well as its sarcous contents, being dissolved; fragments of the fibres, however, pass into the intestine, and there undergo further, though, it may be, incomplete, digestion. Yellow elastic tissue appears to resist the action of the gastric juice; tendinous fibres dissolve slowly; white areolar fibres are totally dissolved. The corpuscles of cartilage are not digested, but the inter-cellular substance undergoes solution. The areolar fibres of adipose tissue disappear, and frequently also the walls of the fat-cells; but their fatty contents are commonly said to resist the action of the gastric juice; fat, however, may begin to be broken up into the fatty acids. (Marcet.) Of vegetable tissues, the cellulose or lignin of the cell-walls, including the dotted, annular, and spiral ducts, for the most part resist the action of the gastric fluid, which is also inoperative upon starch grains, though it does not interfere with, or totally arrest, the action of the swallowed saliva, and of the mucus of the stomach, upon starch. Chlorophyll, the green colouring matter of plants, appears to resist digestion; but the pectinous and albuminoid contents of vegetable cells, are completely dissolved.

Chymification and Chyme.

The general product of digestion in the stomach, resulting from the combined admixture with the food, and the action

upon it, of the saliva, the mucus of the mouth and stomach, and the gastric juice itself, is called the *chyme*; the process of its formation is named *chymification*. The chyme is a thick, pulpy, grumous, fluid, containing the food thus far digested, together with partially digested, and indigestible, matters; it has a strong sour smell and taste, and an acid reaction. The degree of acidity of the chyme varies, however, according to the quantity of acid, such as lactic or acetic acid, in the food, and also according to the relative quantities of saliva and gastric juice contained in it, much gastric juice rendering it more acid, and an excess of saliva less so. The colour of the chyme depends on the food, being whitish in an infant fed on milk and farinaceous food, but of a brownish hue when meat is eaten, or greenish after vegetable diet; sometimes also, it is tinged with bile, which has ascended into the stomach. The presence of saliva, mucus, and gastric juice, is indicated by characteristic microscopic nucleated cells. The composition of chyme, like its colour, also varies with the nature of the food. With ordinary diet, it consists of a mixture of the saline, amylaceous, saccharine, albuminoid, gelatinoid, and fatty matters of the food, in different conditions of conversion or solution. The starch, partly changed into dextrin and sugar in the mouth, continues to undergo transformation in the stomach, even more rapidly, because the vegetable cells are loosened or dissolved, so as to set free the starch grains. The conversion of starch into sugar in the stomach, is due to the saliva swallowed with it, for, in an animal, ligature of the œsophagus, which prevents the continued entrance of saliva into the stomach, arrests this transformation. A good deal of starch always passes from the stomach, undissolved. The albuminoid and gelatinoid substances are represented in the chyme, by albuminose or the albumen and gelatin-peptones; whilst the fatty matters of animal tissues, perhaps to a small extent decomposed, are loosened from the fat cells, and, as well as the fatty matter of butter or cheese, are reduced to minute particles, intermixed with the rest of the chyme.

The characters of the chyme depend, however, not only on solvent actions, but also on the process of *absorption*, which begins in the stomach, as soon as that organ contains fluid or dissolved matters. Owing to the escape of chyme into the intestine, the quantity actually in the stomach, at any one time, is small; and, owing to absorption, the quantity which passes into the duodenum, is much less than the quantity of fluid swallowed

and secreted for the purposes of gastric digestion. Even the soluble constituents of the chyme, are constantly being removed by absorption. The soluble constituents of our solid and fluid food, such as saline matters, sugar, alcohol, and thein, and also the soluble products of digestion, such as sugar, and the albumen and gelatin-peptones, mixed with some salivin and pepsin, are greedily absorbed, with the water of the chyme, by the *blood-vessels* of the mucous membrane of the stomach, and are then conveyed through the portal vein, into the liver.

The chyme itself, therefore, at any one moment, does not represent the simple product of the digestion of food, but the joint product of the double process of digestion and absorption. In comparison with the food taken, it necessarily contains a larger proportion of fatty matter, than of saline, saccharine, amylaceous, albuminoid, or gelatinoid substances; for the fatty substances have undergone little, or no, chemical change, and no absorption from the stomach, whereas the others have been more or less dissolved, altered, and absorbed.

The semi-fluid product is, moreover, constantly being forced forwards, drop by drop, through the pylorus into the duodenum, where it undergoes further changes, now to be considered.

Action of the Bile.

The bile performs a most important part in the intestinal digestive process; but its action does not depend on the presence of an albuminoid substance, like salivin, pepsin, or pancreatin. Its importance is shown by its highly complex composition, and by its containing substances which, unlike the urea and uric acid of the renal excretion, do not pre-exist in the blood, but are formed in the hepatic cells. Secondly, the bile, as already stated, (pp. 74-5), is much more abundantly secreted during the process of digestion than at any other period; and although this may be due to the accompanying activity of the portal circulation, yet the general adaptation of means to ends in the animal economy, suggests the conclusion that the secretion is most required at that particular time. Lastly, the situation at which the bile is discharged into the alimentary canal, immediately below the stomach, and therefore very high up in the intestine, seems to indicate its special adaptation to the further digestion of some important constituent of the chyme. Nevertheless, as we shall hereafter see, a large portion of the solid constituents of the bile, is removed from the body,

and this fluid must, to a great extent, be regarded as an excrementitious fluid, serving to eliminate carbon, hydrogen, and sulphur. The bile also serves certain supplementary non-chemical uses. Thus, it excites the mucous membrane of the intestine, and so probably causes an increased secretion of mucus and intestinal juice. It moreover, stimulates, either directly, or through the nerves, the contractile fibre-cells of the mucous membrane and its villi, as well as those of the muscular coat of the intestine; the former action, probably, promotes absorption by the villi; whilst the latter excites the intestinal peristaltic action, and so aids in the onward movement of the intestinal contents. It is well-known that a scanty supply of bile may lead to constipation, whilst an excess of that fluid induces diarrhœa; hence, it may be inferred, that a proper quantity helps to maintain the healthy action of the intestines. The inspissated bile of the ox is used as an aperient medicine.

As regards the chemical action of the bile, experiments, made outside the body, by digesting various constituents of food in that fluid, at a temperature of 100° , show that it has an exceedingly feeble action in changing starch into sugar; cane sugar is slowly converted by it into lactic acid; it neither dissolves albuminoid substances, nor saponifies or dissolves fat. Albuminoid and gelatinoid bodies, although stained, are otherwise unaltered; fatty matters, agitated with bile, form an imperfect opaque emulsion, but after a time, if left undisturbed, separate themselves entirely from that fluid, unchanged. Bile is said to arrest the actions of saliva and gastric juice, even when these have already commenced, upon starch and albuminoid substances. Indeed, the bile and the gastric juice decompose each other, when mixed out of the body; but this does not seem to be the case, when the gastric juice is already combined with peptone. In living animals, in which biliary fistulæ have been established, so that the bile, prevented from entering the intestinal canal, escapes at the surface of the body, amylaceous, albuminoid, and gelatinoid substances are still completely digested. With regard to fatty matters, however, the bile, appears, in some way, to assist in, or to determine, their absorption. It has been assumed that the bile is a saponaceous compound, and that it dissolves fatty matters directly, like an ordinary soap; but soaps contain more or less free alkali, which assists in dissolving additional fat, whilst the alkaline reaction of bile, even when present, depends probably on phosphate of soda. Experiment shows, however,

that the bile is highly important for the proper digestion of fatty matters. In animals with biliary fistulae, the chyle collected from the lacteals, or absorbents of the intestines, contains but a small quantity of fat; half, or even more, of the fat taken with their food, passes unchanged from the alimentary canal; and, as a consequence of this, the bodies of such animals are very lean. According to the observations of Blondlot and others, animals thus treated, may live even as long as five years. Again, after ligature of the biliary duct in an animal, which prevents the descent of bile into the intestine, the fluid in the lacteals is clear and deficient in fat, instead of presenting its characteristic milky-white colour, and fatty molecular contents. In what mode the bile contributes to the absorption of fat, is not yet known. It certainly does not appear to act chemically, by decomposing or dissolving neutral fats; nor does it make, with oily matters, a permanent emulsion. It probably co-operates with the pancreatic juice. It has also been shown, that fatty matters permeate moist animal membranes more readily than usual, if they be first wetted with bile, or with an alkaline solution. Since provision is made in the saliva and gastric juice, for the complete digestion of amyloid, gelatinoid, and albuminoid substances, and, as we shall presently show, in describing the action of the pancreatic juice, of fatty matters also, the bile may be supposed to possess no exclusive digestive power, but rather to be superadded, in order to complete some particular part of the digestive process.

As the contents of the upper part of the duodenum, like those of the stomach, are strongly acid, whilst those of the small intestine generally, become gradually alkaline in their descent, it was formerly thought that the bile, then regarded as a very alkaline fluid, was concerned in neutralising the acid of the chyme; but it is now known that the bile is but feebly alkaline, or sometimes even neutral, and the alkalinity gradually acquired by the contents of the small intestine, is attributed partly to the pancreatic and intestinal juices, and partly to the evolution of ammonia, from slow decomposition.

The bile not only imparts a bright yellow colour to the chyme in the duodenum, but it further appears to exercise an anti-putrescent action, thus preventing, or retarding, a fetid decomposition of the contents of the intestine; for, in the absence of bile from the alimentary canal, these frequently become decomposed, causing flatulence and diarrhoea. In

does not dissolve them in experiments out of the body. When the pancreatic juice, or the infusion of the gland substance employed, has undergone a kind of putrefaction, such solution may occur; but this is a condition not present in the living body. Moreover, any albuminoid substances macerated in water, will putrefy and slowly dissolve, and such putrefied soluble matter rapidly sets up similar changes in fresh albuminoid substances. Corvisart and Meissner believe, however, that the pancreatic juice is able to peptonise albuminoid substances, but that it only possesses this property when they have been previously mixed with gastric juice and bile, or when they are slightly acidified; or, as Bernard supposes, only after a certain quantity of the digested food has already passed into the circulation, so as to supply the blood with materials suitable for the secretion of some special product, needed for a very powerful pancreatic juice.

Extirpation of the pancreas affords no certain information concerning the use of its secretion. According to some, the removal of the gland is followed by the absence of white chyle in the lacteals, and the presence of undigested fat in the contents of the large intestine; at the same time, emaciation occurs. According to others, when this gland is extirpated, neither a total arrest of nutrition, nor death by starvation, necessarily follow, every constituent of the food still undergoing more or less perfect digestion, the office of the pancreatic juice being fulfilled by other secretions. Complete degeneration of the pancreas in Man, the liver and other organs remaining healthy, does not necessarily interfere with the digestive process; but, in certain diseases of this gland, fatty matter has been observed to pass undigested through the alimentary canal. The use of the pancreatic juice, seems, indeed, to be subsidiary, or complementary, to the other digestive fluids; for it aids the saliva in the conversion of starch into sugar. It is said by some to be able, with the gastric juice, to dissolve albuminoid matters, and if, as is generally believed, its chief office is to digest fatty matters, it must co-operate, in some manner, with the bile.

The effects of the pancreatic juice, on fatty matters, have been shown by experiments out of the body, and by observations on living animals. If either the fluid, obtained fresh from pancreatic fistulæ in animals, or a watery infusion of the substance of the gland just taken from an animal killed during the digestive process, be agitated with a neutral fat, and the mixture be maintained at a temperature of 100°, the fatty

substance is most perfectly emulsified, the action being much more complete and durable than if saliva, bile, intestinal juice, or any other animal fluid, had been employed. The emulsion lasts as long as eighteen hours, after which the fat separates. It is found, however, that a portion of the olein, margarin, and stearin, is now decomposed, having been rapidly separated into the corresponding fatty acids and glycerin. These effects are most marked when the pancreatic juice is collected a short time after digestion has begun, all the characters of the secretion being then most evident.

This remarkable decomposition is usually attributed to the pancreatin, combined with the operation of the free alkali of the fluid, just as pepsin with an acid, effects the transformation of albuminoid substances. The pancreatic juice no longer possesses this power of decomposing neutral fats into their fatty acids and glycerin, in the presence of ordinary acids, which destroy its alkalinity; hence it has been urged, that the acidity of the chyme must prevent this peculiar decomposition. But the pancreatic fluid and the intestinal juice are strongly alkaline, and moreover, the bile may here interpose, and, by means of the soda present in combination with its conjugated acids, may neutralise the acids of the chyme, and so permit the decomposition of the neutral fats of the food by pancreatic juice; for this process may not be interfered with by the acids of the bile, which are themselves fatty. That the action of the pancreatic juice is, in some important way, aided by the bile, and conversely, that the action of the bile is seconded by that of the pancreatic juice, is highly probable, from the fact that they are discharged into the intestinal canal so near together, generally, indeed, at a common orifice.

It happens, however, that in the rabbit, the chief pancreatic duct enters the small intestine rather more than twelve inches below the bile duct, which opens as usual a little below the pylorus; another smaller duct also exists, but it is almost impermeable. This arrangement has been taken advantage of, in physiological experiments on the use of the pancreatic fluid. The most interesting and important of these, is one originally performed by Bernard, and since repeated by others. A rabbit is crammed with fat, or its stomach is injected with oily matter, and it is afterwards killed, whilst digestion is going on; it is then found that the fatty matters in the intestine, above the entrance of the pancreatic duct, though mixed with the bile, are yet unchanged; whilst below that point they

begin to be emulsified; moreover, the lacteals, or absorbent vessels of the intestine, above the point of entrance of the pancreatic duct, although bile is there mixed with the food, are filled only with a clear transparent fluid, and, indeed, are mostly invisible; whilst, at a point immediately below the entrance of the pancreatic duct, those vessels are charged with their characteristic milk-white fluid, containing fatty particles. To this apparently precise and unexceptionable experiment, it has been objected, by those who dispute the influence of the pancreatic juice in the digestion of fatty matters, that the difference in the contents of the lacteals, above, and below, the entrance of the pancreatic duct, depends upon the time that has elapsed before the animal is killed, after being fed with fat. When this is done within two hours, it is said, that the lacteals given off above the pancreatic duct, are found filled with white chyle; but if the animal be killed from four to six hours after, the lacteals below the pancreatic duct are alone filled. These results are not in accordance with the experience of most observers, who fully confirm those obtained by Bernard. It is further stated by that experimenter, that ligature of the pancreatic duct, arrests the emulsification and absorption of fat, but this, again, is disputed by others. The opposite conditions observed by them, are explained by Bernard, on the supposition, either that the smaller pancreatic duct escaped ligature, or that certain minute glands of the duodenum, in part supplied the place of the pancreas. It has been asserted, that if the small intestine be tied, in cats and puppies, below the entrance of the pancreatic duct, and oil, mixed with milk, be injected into the bowel below the ligature, the lacteals, after a time, become filled with white chyle (Frerichs). It is also said, that after the formation of a pancreatic fistula in a cow, chyle collected from a fistula, subsequently made in the thoracic duct, contains almost as much fat as that of other cows in which no pancreatic fistula has been established (Colin and Lasaigne). Furthermore it is objected, that no large amount of saponified fat, is found either in the contents of the intestine, or in the chyle itself, as might be expected, if the pancreatic juice decomposed the neutral fats, and so rendered them absorbable (Bidder and Schmidt).

To conclude: first, the pancreatic juice exercises a positive power of converting starch into sugar, and so may aid in digestion. Secondly, its digestive power over albuminoid

and gelatinoid bodies, when it is fresh, is very slight, but more marked when it is acidified, or when it co-operates with the gastric juice. Thirdly, it possesses a remarkable power of emulsifying fat, and rendering it absorbable, more marked even than that of the bile. Lastly, whilst, out of the body, it not only emulsifies, but also decomposes the neutral fats into their fatty acids and glycerin, it is uncertain whether this decomposition actually takes place within the body.

A case has been recorded, in which a calf's pancreas, taken internally, aided the assimilation of fat; and, quite recently, preparations of pancreatin made from animals, like those of pepsin long employed, have been administered medicinally.

Action of the Intestinal Juices.

Owing to the mixture of secretions in the intestinal canal, it is difficult to determine the digestive properties of the intestinal juices. Portions of food, enclosed in perforated tubes, have been introduced through artificial openings, into the small intestine, the duodenum being first tied, in order to prevent the saliva, gastric juice, bile, and pancreatic juice, from passing down. Other experiments have been made, by isolating portions of the small intestine and its contents, by including them between two ligatures. Various kinds of food have also been subjected to artificial digestion, outside the body, at a proper temperature, in the juices of the small or large intestine, or with portions of the mucous membrane macerated in water. From such experiments, several conclusions are obvious. The strongly alkaline intestinal juice certainly converts starch into sugar, many believing that this change is chiefly accomplished in the small intestine; sugar itself here also passes into lactic and butyric acids; it acts still more powerfully in the solution of albuminoid substances. Lastly, it is also more or less capable of forming an emulsion with fat, and so of aiding the pancreatic juice, or even of supplying its place. It would seem, therefore, that the intestinal juice operates as an auxiliary digestive agent upon the three principal constituents of our food. Its effects do not appear to be interfered with by those of the other digestive fluids. The action of the secretion of Brunner's glands, and that of the intestinal juice, separately, are quite unknown.

*Changes of the Food in the Small and Large Intestine.
Contents of those Intestines.*

In considering the changes in the food, which occur in any given part of the intestine, it must be remembered, that the fluids, poured into the alimentary canal higher up, are still present, in greater or less quantity, in the intestinal contents lower down, and doubtless exercise some digestive influence. Thus, gastric juice, and even saliva, must be present in the upper part of the duodenum, and more or less pancreatic juice and bile, in the lower part of the small intestine. The venous pulpy chyme, poured from the stomach into the small intestine, is acid, and brownish or variously coloured; but, on its admixture with the bile and pancreatic juice, it assumes a bright yellowish colour and becomes much more opaque, owing to the addition of the biliary colouring substances, the decomposition of the acids by the bile, and the gradual emulsification of the fatty substances by the pancreatic juice. The contents of the upper part of the small intestine are still acid, partly from the acid of the gastric juice, and partly from the acids of the bile, which are set free by the former; but their acidity is gradually diminished, not only by the alkaline pancreatic juice, but also, and chiefly, by the even more powerfully alkaline intestinal juice. The hydrochloric acid of the gastric juice, is probably soon neutralised, and is then absorbed into the blood, as chloride of sodium or common salt. At the lower end of the ileum, the reaction of the residual intestinal contents, is generally stated to be alkaline; but near that point, in a case of accidental fistula in the human subject, it has been found acid, notwithstanding the alkaline condition of the mucous membrane. The contents of the cæcum are said to be acid; but those of the large intestine generally, to be alkaline. Much, however, depends on the nature of the food; for, from the formation of acetic or lactic acid, during the use of an excess of vegetable diet, the contents of the whole intestinal canal may be acid. In carnivora, the contents of the cæcum, from the presence of ammonia, exhibit an alkaline reaction, whilst in the herbivora, they are always acid, from the presence of lactic acid.

The chemical composition of the contents of the small intestine, is dependent on the nature of the food taken. It must also vary at different parts of the canal, according to the

composition and quantity of the secretions mixed with it, and according to the relative quantity and nature of the substances which have been absorbed from it. Thus, the contents of the first part of the duodenum, consist of the acid chyme, with bile and pancreatic juice, *i. e.*, of a mixture of the food taken, whether this be bread, milk, meat, or eggs, together with saliva, gastric juice, bile, pancreatic juice, and mucus, minus a certain amount of the water and dissolved substances, which have already been absorbed. These substances, which are almost exclusively absorbed by the blood vessels, consist of saline matters, unaltered starch, sugar, whether pre-existing in the food, or produced by conversion of starch, dissolved albuminoid and gelatinoid substances, in the shape of albuminose and gelatin-peptone, salivin, pepsin, creatin and other extractive matters, and lastly, traces of alcoholic, etherial, acid, and various sapid, substances. The sugar found *here*, is said, by some, to be grape sugar, the conversion of cane sugar into grape sugar being chiefly accomplished, in this part of the alimentary canal, by the agency of the intestinal juice. No fatty matter is yet absorbed, but it all remains in the contents of the upper part of the duodenum. Even after the admixture of the bile and pancreatic juice, all the substances, just enumerated, still continue to undergo solution and absorption, and the fatty matters, also now emulsified and rendered absorbable, are gradually taken up, together with some of the fatty acids of the bile. The contents of the small intestine are thus progressively robbed of all their dissolved or emulsified nutrient substances, in which they become by degrees poorer. Finally, passing into the large intestine, they acquire a greater consistence and a darker hue.

The contents of the large intestine have been supposed to undergo an imperfect secondary digestion in the cæcum; and there are reasons for believing, that such a process, due to the action of lactic or other acids and of the intestinal juices, may, especially after heavy meals, be continued along the rest of the intestine. This may explain the digestion and absorption of the nutrient substances in enemas, by means of which the system, as is well known, may be for a long time supported. Whether starch is changed, or fat emulsified, is uncertain. The final residue consists chiefly of the insoluble or undigested portions of the food, broken down into small fragments. In it are found, particles of vegetable matter, such as unaltered starch-grains, woody fibre, remains of vegetable epidermic,

and other cells, with portions of spiral and annular ducts. Of animal substances, there are present, portions of yellow elastic tissue, cartilage cells, unchanged fat, epidermoid, and epithelial cells, unchanged fragments of fibrous tissue, such as portions of tendon or fascia, and muscular fibres more or less altered, though having escaped complete digestion; besides this, there are certain earthy salts, especially the ammonio-magnesian-phosphate, with the phosphates of magnesia and of lime. The neutral salts of the vegetable acids, such as the citrates, tartrates, malates, and benzoates of potash or soda, appear partially in the contents of the lower part of the large intestine, as carbonates, the rest having been absorbed, also, it is said, chiefly in the form of carbonates. Furthermore, the fæcal mass contains colouring matters and other substances left from the almost completely changed or decomposed bile, such as cholalic and choloidinic acids, traces of cholesterin, and especially the substance named dyslysin, also a crystallisable substance containing sulphur, named *excretine* (Marcet), traces of stearic, margaric, and a peculiar fatty acid called *excreteric* (Marcet), with some animal matter, probably the residue of the pancreatic and the mucous secretions, especially of those of the larger intestine. It appears certain, indeed, that the glandular apparatus of the intestines, serves to excrete, and thus eliminate from the blood, products of the decomposition of the tissues, which would be injurious if retained in it; these must be present in the fæcal substance, and may in great part explain its odour. The small intestine, with its villous mucous membrane, is adapted to the function of absorption; but the non-villous mucous coat of the large intestine appears better adapted for excretory purposes. The percentage composition of the ashes of the daily quantity of fæculent matter removed from the body, varies, according to the food, from 2 to 10 oz.; the average quantity is about 6 oz., of which three-fourths are water. The percentage composition of the ashes, after burning, is as follows:—

Chloride of sodium, alkaline sulphates, and phosphate of soda (or potash)	4
Phosphate of lime and phosphate of magnesia	81.5
Sulphate of lime	4.5
Phosphate of iron	2
Silica	8

 100.

The contents of the stomach invariably include a certain

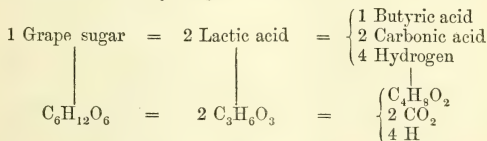
quantity of atmospheric air (4 nitrogen to 1 oxygen), which has been mixed with the food and saliva in the mouth, and swallowed with them. The decomposition of the amylaceous and saccharine food, into lactic and butyric acid, may cause the evolution of carbonic acid and hydrogen. The oxygen, and especially the carbonic acid, being more soluble in water, would be more easily absorbed than the nitrogen and hydrogen; but the nitrogen may also pass into the blood. An interchange of the other gases with carbonic acid from the blood, may take place, by what might be termed *intestinal respiration*. In the small intestine, the carbonic acid and hydrogen relatively increase in quantity, the nitrogen remaining about the same; whilst the oxygen disappears. On including a loop of the small intestine of a living animal, between ligatures at two different points, the gases of the blood, oxygen, carbonic acid, and nitrogen, have been found to pass into the interior of the intestine; so that these gases may be both absorbed from, and excreted into, the intestinal canal. In the large intestine, besides carbonic acid, as the principal gas, carburetted hydrogen may appear, owing to the slow decomposition of its contents; nitrogen abounds after a flesh diet, and hydrogen after a milk diet; lastly, though, it would seem, but seldom, as a consequence of the decomposition of the albuminoid substances containing sulphur, or of the taurin of the bile so rich in that element, or possibly from the de-oxidation of sulphates, small quantities of sulphuretted hydrogen gas are evolved. These two last-mentioned gases may also be absorbed into the blood; indeed, it has been shown experimentally, that animals may be quickly poisoned by injecting sulphuretted hydrogen into the large intestine.

The time taken by different articles of diet to descend through the alimentary canal, varies. Laxative medicines may pass in four hours, carbonate of iron in twelve hours, the colouring matter of spinach and other vegetables in eighteen hours, and grape-pips and cherry-stones in from three to four days. It has been shown that it is useless, and perhaps imprudent, to administer purgatives *immediately after* the accidental swallowing of buttons, coins, or stones; it is better to administer thick tenacious food for a day or two, and then give a dose of castor oil.

Summary of the Chemistry of Digestion.

We have seen that the digestible and absorbable parts of food, consist chiefly of the carbohydrates, or the amylaceous, gummy, and saccharine substances; of hydrocarbons, or fats and oils; of nitrogenous gelatinoid and albuminoid substances, and extractive matters; of hydrocarbonaceous alcohol and organic acids; of saline substances, and of water.

Part of the *starch* is converted, by the saliva in the mouth, into glucose or *grape sugar*; this change still goes on in the stomach, even in the presence of the gastric juice; it is completed, or, according, to some, chiefly accomplished, in the interior of the small intestine, by the continued action of the saliva and by the superadded agency of the pancreatic and intestinal juices. Cooked starch is changed more rapidly than raw starch, the cells of which sometimes escape digestion; the emptied envelopes of the starch grains commonly remain undigested. Cane sugar (Bouchardat), and milk-sugar (Lehmann), are for the most part converted into grape sugar, in the stomach, more particularly in the intestine; small quantities of cane sugar are said to be absorbed without change (Bernard). The grape sugar, thus formed from starch and other sugars, or that which may be contained in the food, is principally absorbed as such by the blood vessels; but it appears partially to be changed, especially when abundantly taken, within the alimentary canal, into lactic acid, and this again into butyric acid, with an accompanying separation of carbonic acid and hydrogen. Thus:—



The *albuminoid* bodies begin to be digested in the stomach, by the gastric juice; whilst their solution is continued, and completed, in the small intestine, by the additional action of the intestinal juice. Fluid albumen, and especially vegetable albumen, and coagulated fibrin, are easily digested; coagulated albumen, casein, gluten, and legumin, more slowly. Casein is first precipitated in a flocculent form, and then dissolved.

All albuminoid substances are converted at once into albuminose or albumen-peptone. Gelatin and gelatin-yielding tissues are converted into gelatin-peptone. These peptones, and also the saliva, pepsin, and pancreatin, are absorbed from the stomach, as well as from the small intestine, and chiefly by the blood vessels.

Fats, whether pure, and merely melted by the heat of the stomach, or whether forming part of an organised tissue, and set free by the digestion of the enveloping areolar tissue and walls of the adipose cells, coalesce, into small drops, in the stomach and upper part of the duodenum. In the small intestine, so long as its contents remain acid, the fats are merely emulsified by the pancreatic juice, aided possibly by the bile; in the lower portion of the small intestine, however, where the intestinal contents become more or less alkaline, certain quantities of the fat are probably decomposed into their fatty acids and glycerin, by the further action of the pancreatic juice, and may even be saponified by the strongly alkaline intestinal juice. Thus emulsified, decomposed, or saponified, all but a small residue of the fatty matters are absorbed by the lacteals of the intestines.

Alcohol, in all its forms, *ethers*, and other soluble *acid* and *sapid* bodies are absorbed unchanged, along the whole surface of the alimentary canal, chiefly, if not entirely, by the blood vessels. This absorption begins even in the mouth, otherwise these substances would produce no flavour. The organic acids probably decomposed into carbonates.

The *extractive* matters, creatin and creatinin, the cerebrie acid, those which are uncrystallisable, and perhaps some of the cruorin and myochrome, are also probably absorbed without change, by the blood vessels.

The *saline* constituents of the food are chiefly absorbed without alteration; the soluble ones, from the mouth, stomach, and intestinal canal generally; whilst the less soluble phosphates of magnesia and lime, appear rather to be dissolved in the large intestine. Any carbonates contained in the food or drink, must be decomposed by the acids of the gastric juice, by the lactic acid of the food, and by the acids resulting from the decomposition of saccharine matters. The salts formed by such organic acids with soda or potash, are either absorbed into the blood, and there converted into carbonates, or they are thus changed in the intestinal canal.

Water remains undecomposed, and is absorbed freely during

the digestive process, constituting the natural menstruum, in which the different soluble substances are dissolved, and in which the fatty matters are suspended.

Of substances, the digestion of which is doubtful, may be mentioned vegetable-mucus, gums, pectin, and cellulose. The three former, though soft and tender substances, miscible but probably not actually soluble in water, are said, by some, indeed, neither to be capable of being absorbed, nor yet to be so chemically changed, as to become so. The softer kinds of cellulose, such as that contained in the growing tissues of green vegetables, in the tuber of the potato, and in the pulp of fruits, are supposed to be dissolved in small quantity, if not for nutrient purposes, yet in order to set free their starchy, gummy, saccharine, and albuminoid contents. Herbivorous animals, however, certainly digest large quantities of cellulose and vegetable pectin, by changing them into sugar. Chlorophyll, speaking generally, is indigestible. Though putrescent meat, such as high game, may be first sweetened, and then digested by the gastric juice, yet certain decomposing substances, like poisonous or fermenting sausages, cannot be corrected by the juices of the stomach, but excite vomiting and diarrhoea, and, when absorbed, often prove fatal.

Circumstances which modify Digestion.

The rate of gastric digestion of certain articles of diet, has already been mentioned (p. 92). It partly depends on the relative solubility of the various proximate constituents of the food; but it may also be greatly modified by other circumstances, such as the quantity, consistence, and peculiar mixtures of the food, its condition of subdivision, its absolute quantity, the relative quantity of its different constituents, the absence or presence of stimulating substances, the conditions of the nervous system, the state of sleeping or waking, the condition of the body as regards health, habit, individual peculiarities, bodily fatigue, and even the condition of the mind. Rest and exercise also affect the digestive process.

The more rapidly and perfectly the constituents of any given kind of food, are capable of being dissolved, the more easily such food is digested, and *vice versâ*. As a rule, bread, not too new, nearly all kinds of meat, poultry and white fish, eggs, milk, jelly, and the gelatin-forming tissues, and well-boiled potatoes, are easy of digestion; whilst new bread and potatoes,

fatty meats, fat, tendons, cartilage, cheese, and green vegetables are more difficult of digestion. Hard-boiled eggs are, of course, more difficult to digest than the fine coagulum of albumen formed in a custard, or in the gravy of meat, owing obviously to the difference of consistence and degree of subdivision in the two cases. Mashed potatoes and finely grated cheese, and soft cream- and milk-cheeses, are more easily and rapidly digested than plain boiled potatoes or hard cheese. Again, all vegetable substances too much matured, and therefore composed of cells having harder cell walls, are more difficult to digest, and hence require much cooking, and artificial subdivision, to burst and break down the cells, and permit the digestive juices to enter their interior, and act on their contents. Carrots, turnips, cabbages, celery, artichokes, asparagus, and onions, may be classed in this category. Even the cooking of flour, and of all other amylaceous articles of diet, helps digestion in an extraordinary degree, by bursting or swelling the fecula or starch grains. Large quantities of adipose tissue, intermixed with muscular tissue, probably impede the penetration of the gastric juice, and so render too fat meats, such as pork, and also oily fish, as, for example, salmon, comparatively indigestible. It has been found that the flesh of animals living in a wild state, is more digestible than that of the allied tame species, probably owing to the more fatty muscular tissues of the latter. A large quantity of fat, in the shape of fatty tissue, taken with other food, may have the same effect of interfering with digestion; but such fatty tissue is far preferable to fat itself, and more easy of digestion, because it is contained in areolar tissue, and is divided into minute spherules within the fine adipose cells, so that the gastric juice percolates it with comparative facility. Hence suet and cooked fat are more digestible than the melted fat derived from them, and swimming on the surface of gravy. Pure solid fats having a granulated texture, especially cold butter, the particles of which adhere together, as it were, only by certain points of contact, are more easily digested than the same fats taken in a melted condition, such as oiled butter, in which, the oleaginous particles have completely coalesced. It is possible, also, that the heating of fatty matters determines slight chemical changes, inconsistent with easy digestion. But perhaps the most objectionable effect of fat, is that which occurs in certain processes of cooking, in which it saturates heated or dried albuminoid, gelatinoid, or amylaceous substances, and

so preoccupies their interstices, as to render them extremely difficult of penetration by the gastric juice, which is aqueous, as in the case of buttered toast, or greasy hot dishes of any kind. Moreover, owing to the high temperature in roasting or baking, the substances above mentioned, as well as the fats themselves, sometimes undergo peculiar chemical changes, by which acrolein, or other pyrogenic compounds are perhaps developed. These latter conditions are met with in the burnt parts of roasted joints, in over-roasted, baked, or fried parts of the skin of poultry or of fish, and especially in greasy and burnt pie-crust.

It would seem that animal albuminoid substances, held in solution, as in soups and broths, are not more easily digested than the same substances in a solid form; for the water requires to be almost entirely absorbed, before the nutrient principles can be converted into peptones. Hence, solid food, even in the case of many invalids, is more suitable than bulky fluid food. It is said that dextrin, introduced into the system, favours the digestion of albumen (Schiff); this affords an illustration of the advantage of mixed diets.

Too large a quantity of food, at any one meal, also renders digestion proportionally difficult. When the digestive powers are weak, the bad effect of quantity is much more obvious. It is believed that the secretion of the gastric juice especially, is regulated, as to quantity, more by the demands of the body, than by the amount of food taken; hence, an excess of food, not only remains undigested, but acts as an irritant to the stomach itself, lessening its further secreting power, and, if passed on into the duodenum, causing more or less disturbance to the system. At the same time, some solid substance is essential or favourable to digestion; hence, perhaps, the habit of certain nations, mixing, with their scanty food, some indigestible material, such as saw-dust or earth, which can only increase its bulk. After a very heavy meal has been digested, the stomach secretes but a very weak gastric juice (Schiff).

The effects of cold water, or ice, in repressing the secretion of the gastric juice, and so retarding the digestive process, have been already mentioned; the reduction of the temperature of the stomach, and the retardation of the capillary circulation, afford an explanation of these facts; taken in large quantities, with or after food, ices and iced beverages must suspend digestion. On the other hand, digestion is undoubtedly favoured by moderate quantities of alcohol, also by

salt, vinegar, lemon juice, pickles, sauces, and spices, these substances acting as stimulants to the secreting processes necessary for digestion, especially to that of the gastric juice; vinegar, moreover, contributes, by its acidity, to swell and pulpify albuminoid substances. Lemon juice yields, in addition, potash salts to the blood. Wines and beers also contain potash, magnesia, and lime; the red wines especially, yield small quantities of tannin, and traces of iron.

Severe exercise of the body, or active employment of the mind, too soon after a meal, hinders digestion; even moderate exertion of the body is not desirable immediately after a full meal, rest being found decidedly to favour digestion; but persons of sedentary habits digest slowly. Sleep is said to retard this process, but otherwise does not interfere with it. Mental emotion may arrest digestion, perhaps, by putting a stop to the secretion of gastric juice. Digestion, as already mentioned, requires, for its due performance, the secretion of large quantities of the digestive fluids, and this can only be accomplished by an increased supply of blood to the organs concerned in this function; hence, any acts which determine the blood strongly to the brain or muscles, interfere with it.

Habit has an extraordinary effect in modifying the digestive power in particular instances; thus, infants or invalids, who have been habitually fed on fluid and easily digested food, are inconvenienced, or injured, by the use of hard food difficult of digestion, and can only by degrees acquire, or regain, a stronger digestive power. Those persons, even, who are accustomed to take food of a dry and hard nature, and requiring strong digestive powers, have their digestive organs deranged by the use of soft and succulent food, which they can only properly digest after a kind of education. A certain effort in the digestive act, is probably beneficial, as it is natural to the system.

Custom, and differences of climate, explain the well known national peculiarities of diet, and also the fact that, as a rule, a foreign dietary, unless modified, or gradually adopted, is less adapted to the digestive powers of individuals of different nations and climates.

Finally, the effects of individual differences, or, as they are called, *idiosyncracies*, are truly remarkable in the case of the digestive functions. In certain instances, particular, and perhaps not otherwise difficultly digestible, substances invariably produce the most serious pain and disorder; whilst substances ordinarily indigestible, may perhaps be readily digested.

Thus, for example, oysters, lobsters, crabs, and salmon, will each produce, in different persons, severe attacks of indigestion, and even give rise to eruptions on the skin. In some persons, strawberries are known to produce a similar effect; and to others, cucumber is almost a certain poison.

Relative Value of different Foods.

The following Table, chiefly from Vierordt, exhibits the composition of a few of the great variety of articles of food consumed by Man. It shows the total amount of solids, and the proportions of organic proximate constituents, salts, and water, in each article of diet; also the relative amount of its nitrogenous and non-nitrogenous constituents, and, as regards the latter, the respective quantities of oleaginous, amylaceous, and saccharine matters. The relative value of different articles of diet, for plastic or tissue-forming purposes, for calorific or respiratory purposes, or for maintaining the proper saline constitution of the blood, is thus shown, so far as their chemical composition is concerned; but this alone affords no sufficient indication for the practical choice of diet in individual cases, so much depending on the physical characters and mode of preparation of food, as well as on the age and idiosyncracies of the individual.

The total quantity of solids, shown in the first column of the following Table, reveals the highly nutritive quality of leguminous and cereal food, butter, cheese, and eggs, in comparison with meat; but such general comparisons are inexact, for the proportions of non-nitrogenous and nitrogenous substances, in each kind of food, are not taken into account. As regards the latter, cheese is the most nutritious diet, then the leguminous seeds, next meat, and then, in order, the yolk of egg, flour, the white of egg, and bread. As regards fat, the order of nutritive value is, butter, yolk of egg, and cheese. Starch and sugar are most abundant in wheat, next in the leguminosa and the inferior cereals, less so in potatoes, and least in the succulent vegetables and fruits.

Cheese is an extraordinarily concentrated diet; the leguminosa are highly nutritious, especially those grown in hot countries, but they require a thorough preparation and good cooking; the great merit of bread, is its soft, porous, permeable, and well-cooked substance; the advantage of meat consists in its concentrated, yet succulent, tender, and easily digested

substance, and in its containing the very elements of the tissues and the blood, even fat, creatin, and the potash salts. Potatoes are a weak food, one pound being only equal to about six ounces of bread, and four ounces and a half of lentils; they are not much more nutritious than the succulent vegetables, but, like these and fruits, they contain, which bread does not, potash, so essential to the muscles; hence, perhaps, their utility in preventing and curing scurvy.

A well selected vegetarian diet is quite equal to the maintenance of life and health; the Japanese, the Hindoos, and the lazarroni of Naples, subsist chiefly on a vegetable diet. The macaronis and vermicellis are composed of gluten, with but a small proportion of starch. Indian corn, and also wheat, though not in such quantity, contain cerebrie acid, a remarkable nitrogenous compound, found in the nervous substance, of very high atomic constitution. Broth is a very weak nutriment, even when some strong farinaceous element is added to it; so is beef tea, if improperly prepared. Meat contains principles which may be extracted, some better by cold water, others by warm water, and others, again, by boiling; it should, therefore, be cut into small pieces, be submitted for three hours each time, in succession, to half its weight of *cold*, of *warm*, and of *boiling* water; the fluids, strained off from the first and second macerations, are to be mixed with that strained off hot from the third or boiling process, and the mixture should be just brought to a boiling heat to cook it; the fat should be skimmed off; a few drops of some acid, with salt, will increase the flavour. Thus prepared, beef-tea contains albumen, traces of syntonin, fibrin, cruorin, and myochrome, in a flocculent state; and gelatin, creatin, cerebrie acid, perhaps glycogen, inosite, paralactic, lactic, and inosinic acids, and salts of potash, soda, and magnesia, in a state of solution; nearly all the syntonin remains in the shrunken meat; the fat is never absolutely removed. Beef-tea, if good, is a light, nutritious, easily assimilated, conservative, and stimulating food. The now much used *extractum carnis* or *extract of meat*, is the inspissated juice of meat, and resembles a viscid beef-tea; but it contains no gelatin, and no glycogen or sugar; to be truly nourishing, it requires the addition of some albuminoid and amylaceous materials. Malt liquors are more nutritious than weak beef-tea. Alcohol stimulates, and develops heat; it seems to be partly digested and oxidised, though a great portion escapes unchanged by the lungs, skin, and kidneys.

Food.	Total Solids.	Albuminoids.	Gelatinoids.	Fatty.	Starchy, Saccharine, Gummy.	Cellulose, Lignin.	Extractives, &c.	Salts.	Water.	Remarks.
Meat . . .	26	Sy. 16, Al. 2	2	3			2	1	74	Also Myochrome and Crnarin, and often Glyco- Strong broth, 3 per cent. of solids. [gen. The Starch is Glycogen. Cerebric Acid. The white is twice the weight [of the yolk. Some volatile fatty acids.
Broth (common)	1.5	Small	.5	Small			.3	.3	98.5	
Brain . . .	24	Al. 8		15			?	1	76	
Liver . . .	29	Al. 13.5	5	3.5	St. or Su. 1-2		4	1	71	
Egg, yolk . .	48	Vit. 17		29			1	1	52	
Egg, white . .	15.5	Al. 11		1-2	Su. traces.		2	.5	84.5	
Milk. . . .	13	Cas. 4-5		4	La. 4			.5	87	Indian corn especially contains Cerebric Acid. Some of the Sugar is Inosite. Organic Acid 1. Organic Acid .5-1. Organic Acid .7
Cheese . . .	62	Cas. 33		24					38	
Butter . . .	78.5	Cas. 1.5		77				5	21.5	
Wheat Flour .	98-87	Gl. & Al. 13		1	St. 61	3.5		1	12-13	Organic Acid .5, Phosphates. Alcohol 5-12, Ether, traces. In Red Wine, Tannic Acid. Alcohol 2-5. Oil of Hops.
Wheat Bread .	57	Gl. & Al. 9			St. 34, Dex. 11, Su. 2			1	43	
Rye Bread . .	55.5	Gl. & Al. 9			St. Su. & Dex. 40	5		1.5	44.5	
Peas. . . .	86	Le. & Al. 23		2	St. Dex. & Su. 53	4	2	2	14	
Lentils . . .	89	Le. & Al. 27		2.5	St. Dex. & Su. 56	2	?	1.5	11	
Potatoes . .	26	Al. 1-2		1.5	St. 13, Dex. 2	6	1.5	1	74	
Carrots . . .	15	Al. 1.5		.3	Su. & Dex. 8	3		1.5	85	
Cabbages . .	21	Al. 2		.3	Su. & Dex. 14	3	2	.5	79	
Apples . . .	18	Al. .5			Su. & Dex. 8	8		.7	82	
Cherries . .	25	Al. .7			Su. 8-11	1.3		.5	75	
Grapes . . .	19	Al. .7			Su. 15	1.5		.5	81	
Wine . . .	14-8	—			Su. .5		.3	.2	86-92	Organic Acid .5, Phosphates. Alcohol 5-12, Ether, traces. In Red Wine, Tannic Acid. Alcohol 2-5. Oil of Hops.
Beer. . . .	10-7	Traces			Su. & Dex. 6			.2	90-93	

Abbreviations.—Al. Albumen; Sy. Syntonin; Cas. Casein; Vit. Vitellin; Gl. Gluten; Le. Legumin; St. Starch; Su. Sugar; Dex. Dextrin;
La. Lactin.

THE ORGANS AND FUNCTION OF DIGESTION IN ANIMALS.

The process of digestion, by which food is dissolved and rendered absorbable by the living body, is almost universally performed by animals; and a digestive apparatus is found in nearly all animals, a few Entozoa and most Protozoa excepted.

The general idea of such an apparatus, is an internal digestive cavity, communicating with the exterior. The plan of construction of this internal receptacle, presents a general resemblance in each separate Sub-kingdom, but in each, it offers further modifications. These are the most varied and detailed in the Vertebrata, but they exist also in the Mollusca and Annulosa, and may be traced in the Molluscoida, Annuloida, and even in the Cœlenterata. In the Vertebrata, the plan is not only modified in each Class, but, in the Mammalia especially, it presents peculiar adaptations, suiting it to the carnivorous, insectivorous, frugivorous, herbivorous, omnivorous, and marine habits of the animals composing its several Orders. The digestive apparatus becomes, indeed, like the rest of the economy, more complex as we ascend in the animal scale; and its diversities of form and structure become most obvious in the highest groups.

The digestive cavity usually takes the form of an *alimentary canal*, which, in its perfect condition, presents two orifices, an inlet, and an outlet. It is usually divisible into an œsophagus or gullet, a stomach, and an intestine. Its relative length and capacity, and the complication of its superadded parts in any given case, have reference chiefly to the nature of the food. Thus the vegetable-feeding species of any group, be it Order, Class, or Sub-kingdom, have a longer, more capacious, and more complicated apparatus, than their congeners which live upon animal food. This fact is illustrated by comparing the snail with the oyster, most insects with spiders, the caterpillar with the perfect insect, the tadpole with the perfect frog, the vegetable-feeding turtles and tortoises with the carnivorous fishes, the granivorous with the carnivorous birds, and the herbivorous with the carnivorous quadrupeds.

It is said that the intestine of the domestic cat, is longer than that of the wild cat, and even that the same is the case with the vegetarian races of men, as compared with men generally. The greater length and complication of the alimentary canal in vegetable feeders, are owing to their food requiring more prolonged digestion than an animal diet; its increased capacity is due to the fact, that to obtain a given quantity of nutriment capable of supporting life, a greater bulk of vegetable food is required than of animal food, particularly so, when that consists, not of fruit and seeds, but of grasses, or the green parts of herbs and trees, as is the case with the food of the Ruminants, Solipeds, and Pachyderms.

The digestive apparatus is also modified to suit the physical condition of hardness or softness of the food, and the various modes in which the animal must seize, crop, and masticate it; hence the existence of modifications in the prehensile and masticatory apparatus, the mouth, teeth, and gizzard. Furthermore, the periods of feeding influence the form of the digestive organs; animals of the same order, Ruminants for example, which feed constantly, having a simpler construction of the stomach than those which, by instinct or necessity, take food or drink at

longer intervals ; hence the great capacity of the stomach and large intestine in the Ruminants, Solipeds, and Pachyderms generally, the existence of water-cells in the paunch of the camel, and the presence of large crops in many granivorous birds. In the Class of Birds generally, an example is met with of a modification dependent on the plan of the Class itself ; for a heavy external masticating apparatus, connected with the head, being inconsistent with the organic aim of construction for flight, an internal crushing apparatus, or gizzard, is present where the food requires it.

Prehension of Food in Animals.

Mammalia.—The prehensile limbs of the Quadrumana seize the food, and transfer it to the mouth. In the feline tribe, the paws serve to capture living prey, but do not convey it to the mouth, this being accomplished by movements of the head and jaws. In many Rodents, as in the squirrel, rat, mouse, and guinea-pig, and also in the kangaroo, and other Marsupials, the two anterior limbs are often used together for holding food, and approximating it to the mouth. In most Mammalia, however, the anterior limbs are organised for locomotion, and the jaws and teeth are the instruments used for capturing or cropping the food, and for its introduction into the mouth. In all cases, the lips are employed. The act of sucking, characteristic of all young Mammalia, and that of drinking in the adult, is performed by the lips, cheeks, and tongue, and the lapping of the Carnivora, by the latter organ only.

Special contrivances for the seizure of the food, are noticed in the snout of the tapir, the proboscis of the elephant, the long tongue of the giraffe, and the extensible viscid tongue of the ant-eaters. The marine and piscine Cetacea, have either rudimentary or no limbs ; some, like the dolphin and porpoise, seize their prey by means of their many-toothed jaws ; the whale-bone whale opens its huge mouth, as it moves through the water, which, entering that cavity, filters through the numerous whale-bone plates, descending from the upper jaw and fringing the sides of the mouth, and so leaves multitudes of soft marine creatures, Pteropods and others, in the interior of the mouth, ready to be swallowed ; lastly, the vegetable-feeding dugong employs its lips and jaws. The ornithorhynchus takes its food by its duck-bill horny mandibles. In a few Mammalia, as in certain Quadrumana, Bats, and Rodents, cheek-pouches exist for the temporary reception of food ; these are very large in the hamster and opossum.

Birds.—The raptorial species, and also the parrots, use the foot prehensively, as well as the jaws. In most birds, however, the bill is the substitute for the tooth-bearing jaws and fleshy lips of the Mammalia, and the shape of this most characteristic part in Birds, is variously modified to suit the character of the food. Thus, it is short and strong in the granivorous sparrows and linnets ; long and tender in the small insectivorous warblers and fly-catchers ; notched in other insectivorous birds, as in the shrikes ; short and gaping in the swallows and night-jars, which catch their prey upon the wing ; strong and hooked in the rapacious eagles and vultures, which tear up their food ; long, conical, and of great strength, in the digging rook, and in the wood-peckers, which pierce the bark of trees ; short, curved, and of great depth in the

parrot tribe, which can crush hard nuts; exceedingly delicate and tapering in the humming birds, to enable them to penetrate the tubular corollas of flowers; ponderous and ungainly in shape, in the toucan and the adjutant; long, strong, and pointed, for the catching of fish, in the herons, storks, and kingfishers; elongated and suctorial, in the snipes and sandpipers, which seek their food in bogs or sands; flattened, grooved, and sensitive, in the ducks, geese, swans, and spoonbills; or it presents still other forms, for holding fish, as in the pelicans, pilgrims, albatross, penguins, and auks. In the cross-bills, the mandibles, when closed, pass by each other so as to present the appearance of a deformity, but this peculiar conformation enables them to extract, with great facility, the seeds from the fir cones. The young pigeon is fed on the regurgitated contents of the crop of the mother-bird. This is accomplished, not, as is usually stated, by the mother placing its bill in the mouth of the young bird, but by the very opposite manœuvre. The lower mandible of the young pigeon, is elongated and boat-shaped, and, for a time, of disproportionate size as compared with the upper mandible; hence it forms a sort of spoon for the reception of the food taken from the gullet of its parent; as the pigeon grows, the lower mandible becomes relatively smaller (Tegetmeier). In the parrots and woodpeckers, the tongue is prehensile.

Reptiles.—These, like birds, have no lips. They capture their prey with the jaws, which are horny in the Chelonians, have small teeth in the Ophidians, powerful teeth in the larger Saurians, and delicate and even complex teeth in the small insectivorous species. The limbless serpents crush their prey in their coils, before swallowing it. The prehensile tongue of the chameleon is well known.

Amphibia.—In these animals, the soft lips and jaws are sometimes provided with minute prehensile teeth; the food is taken by a snapping movement. The tongue of the toad has been already referred to (Vol. I. p. 246).

Fishes.—By these, the food is invariably seized by the jaws, which are usually provided with numerous sharp recurved teeth; though, in some species, the mouth is suctorial, and the teeth are few, or even wanting. In the amphioxus, the oral orifice is guarded with soft *cirri*, whilst the mucous membrane of the mouth is provided with ciliated processes; the food is perhaps conveyed into the mouth by ciliary action.

Mollusca and *Molluscoida*.—The so-called feet of the Cephalopods serve to convey food to the mouth: but the tentacula generally present in Molluscs, are sensory rather than prehensile, the food being seized by the mouth, as in the terrestrial and in certain aquatic Gasteropods, or brought thither by currents of water caused by movements of the mantle, or by cilia, as in the Lamellibranchiata. In the molluscoid Polyzoa, the ciliated tentacles around the oral aperture produce a vortex, by which minute organisms in the water are hurried into the pharynx. In the Tunicata, the cilia lining the fore-part of the alimentary canal, accomplish a similar purpose.

Annulosa and *Annuloida*.—Most Annulosa have distinct buccal appendages, consisting of two pairs of jaws; the first pair are the *mandibles*, or *pincers*; the second are the *maxillæ*, which support the *palpi*. By these parts, the food is seized, examined, or even divided. In many Insects and Crustacea, and in Spiders, one or more pairs of the limbs are

also employed in conveying food to the mouth; sometimes, as in the crabs and lobsters, such limbs are enormously developed, the pincers on one side of the body being smooth, and on the other, knobbed. In certain perfect insects, the food being viscid or fluid, the mandibular appendages are specially modified, as, *e.g.*, in the butterflies and moths, in which they form a long tube or canal named the *proboscis*, which can be unfolded from its spiral coils, and protruded into flowers; a sucking proboscis also exists in certain flies and gnats. In the fleas and bugs, the mandibles are penetrating and suctorial. Amongst the Annelides, the sand-worms have soft feeble tentacles; but the earth-worms and leeches have the mouth either simply suctorial, or cutting and suctorial. In some worms, a retractile proboscis exists, developed from the lining membrane of the pharynx, and not from the cephalic segments of the exo-skeleton, like the jaws of the higher Annulosa. The Annuloid Entozoa either have a special suctorial apparatus, or live by general imbibition. The marine worm-like forms are suctorial, whilst the Rotifera have a ciliated disc, which creates a vortex in the water. In the starfishes and echini, there are no prehensile tentacula; in the Crinoida, the arms may act prehensively; in the holothurida or sea-cucumbers, large labial appendages or tentacula exist.

Celenterata.—These exclusively aquatic animals have contractile non-ciliated tentacles, sometimes few and simple, or divided, as in the hydra, sometimes very numerous, as in the sea-anemones, and often of great length and of irregular form, as in the medusæ and others. These are always prehensile; but food may also be drawn into the body, by the alternate expansion and contraction of its muscular walls. In the Physograda, the mouth is developed into depending tubular suctorial processes or cirrhi.

Protozoa.—In the Infusoria, the cilia draw the water and food into the buccal orifice, and there is no other prehensile apparatus. In the lowly-organised Rhizopods and Amœbæ, the soft body is merely applied to the substance serving as food. In the Spongida, currents of water are drawn through numerous in-current or inhalent orifices, into the interior of the porous mass, whilst ex-current or exhalent orifices, fewer in number, serve for their expulsion. This process not only assists in respiration, but also in entangling food against their sarcodous substance. Finally, the parasitic Gregarinida live by direct imbibition.

The Teeth and Mastication in Animals.

True teeth, or calcified organs, belonging to the exo-skeleton, and composed of *dentine*, or of this with *enamel* and *cement*, are peculiar to the Vertebrata; for the so-called teeth or *denticles* of certain Mollusca, Annulosa, and Annuloida, have no such structure.

Teeth are entirely absent in Birds; but they are generally, though not universally, present, in Fishes, Amphibia, Reptiles, and Mammalia. In the last-named Class alone, are the characteristic *milk* teeth met with, that first temporary and deciduous set, which falls out and is succeeded by the permanent teeth. With the exception of a few fishes, and the vegetable-feeding iguanas amongst reptiles, which have grinding teeth, these organs in Fishes, Amphibia, and Reptiles, are

essentially prehensile, or incisive, being used for seizing, and holding the prey, or for dividing it into portions small enough to be swallowed ; but it is in the Mammalia, that *mastication* proper, performed by teeth set in movable jaws, is most perfect, the food being, in many of them, not only seized, but afterwards gnawed or chewed.

In the different classes of the Vertebrata, the teeth differ remarkably in number, shape, position, and mode of insertion.

Mammalia.—Amongst these, the Monotremata are almost edentulous, or destitute of teeth, for the echidna has no such organs, but merely horny processes on the tongue and palate, whilst the ornithorhynchus has horny teeth. In the Cetacea, two genera have calcified teeth *before birth* only, the upper jaw afterwards supporting the whale-bone plates. In the manis, or pangolin, and in the true ant-eaters, or myrmecophaga, amongst the so-called Edentata, there are likewise no teeth. All other Mammalia possess them.

The *number* of the teeth in the Mammalia, in conjunction with other differences in shape or kind, furnishes an important means of zoological distinction. It ranges from 2 in the narwhal, to as many as 190 in the dolphins. In the elephant, there are at most 10, usually only 6, viz. one entire molar, or sometimes parts of two, on each side of both jaws, together with the two tusks of the upper jaw. In the Rodents, the ordinary number is 20, but there are sometimes only 12, and in the hare and rabbit 28. In the Ruminants, in the apes of the Old World, and commonly throughout the Mammalia, as in Man, there are 32, but 44 is said to be the typical number. (Owen.) In one of the armadilloes, as an exception to the rule in that genus, there are 98 teeth. Amongst the Cetacea, the narwhal, just mentioned, and some other species, have only 2 teeth ; the cachalot has more than 60, the common porpoise between 80 and 90, and the true dolphins from 100 to 190.

The *form* of the teeth presents greater variety in the Mammalia than in any other Class. When numerous, they are usually prehensile, small, pointed, and of nearly equal size throughout the jaw ; sometimes slightly recurved, and sometimes variously flattened or compressed. When the teeth are in moderate number, some are devoted to one purpose and some to another, and they are usually modified into incisor, canine, premolar, and molar teeth. The incisors, as in Man, are flat, chisel-shaped, and cutting or gnawing ; the canines are larger and conical, to bite, hold, and tear ; the premolars and molars are variously cusped or tuberculated, and either flattened at the sides for cutting, or broad at the summit for grinding the food. The incisor teeth are smallest in the insectivorous, larger in the carnivorous and frugivorous species, of great strength in the cropping Herbivora, but especially strong in the gnawing Rodentia. The canine teeth, prominent in the carnivorous dogs and cats, are also large in many non-carnivorous animals, as the ape, boar, musk-deer, elephant, and others, in which they are used for offence or defence. The carnivorous molars are generally flat, narrow, ridged and tuberculated, the anterior ones being often very diminutive. The herbivorous molars are flat-crowned, quadrangular, or lozenge-shaped, and provided with tubercles, as in the Quadrumana, or marked with crescentic or transverse ridges and furrows, as in the Ruminants, Solipeds, Pachydermata, and Rodents. In animals living on mixed diet, the crowns of the molar teeth are furnished with blunt tubercles. The tusks

of the elephant are huge canine teeth; those of the walrus are also canine. The single tusk of the male narwhal or *Monodon*, several feet in length, is also an upper canine tooth; it springs on one side of the median line, from the superior maxillary bone; but an immature tooth is found concealed in the bone of the opposite side; in the female narwhal, both tusks remain undeveloped, one in each upper jaw-bone. The curved canine tusks of the *Babyroussa* are also remarkable; those of the upper jaw are larger and longer than those of the lower jaw, and sometimes perforate the upper lips.

The teeth in Mammalia are limited to the jaws. They are confined to the inferior maxilla in the cachalot, to the premaxillary bones in the upper jaw in the narwhal, and to the superior and inferior maxillary bones, being wanting in the premaxillary bones, in most Ruminants. But usually, teeth are found in all three of these bones. However varied in number and in form, mammalian teeth are always arranged, in each jaw, in a single row or dental arch, in which, where different kinds of teeth exist, one or more gaps occur, named *diastemata*. When a diastema is absent, the teeth are of equal length. In the human jaw, as already mentioned, there is no diastema, but this is also the case in certain extinct quadrupeds.

The mammalian teeth are usually fitted closely into sockets in the jaws, each tooth and each fang, if these be multiple, having its own socket, lined by a periosteum which fixes it. In certain Cetacea, the sockets are wide and shallow, and the teeth are attached to the gum, rather than fixed in the jaw. Each tooth generally has a constricted part or neck, between the crown and fang, to which the gum is fixed; but no neck is seen in the numerous small teeth of the dolphin, in the tusks of the narwhal, elephant, and walrus, or in the incisors of the Rodentia.

The teeth of most Mammalia, like those of Man, consist chiefly of dentine, the crown being protected by enamel, and the fang being covered by the cement, which sometimes passes over the crown also. The microscopic structure of these tissues, however, presents certain minute peculiarities. The tusks of the narwhal, walrus, and elephant, are destitute of enamel, and consist almost wholly of the modification of dentine known as *ivory*, the surface being at first covered by a thin layer of cement, which becomes worn by use. No enamel exists on the molars of the dugong and cachalot, nor on the teeth of the Edentata. In the Quadrumana, and in the Carnivora generally, as in Man, the cement is so thin over the enamel of the crown, as to be almost inappreciable; but it is thick in Herbivora, and especially so on the molars of the elephant, sloth, dugong, walrus, and cachalot. In the Ruminants, in most Rodentia, and in the Pachydermata, the enamel and the cement are arranged, within the crowns of the molar teeth, in double vertical plates or folds, between corresponding processes of the dentine, the variations in which, form a means of classification in the Rodentia and Pachydermata.

When one of these compound teeth, such as a molar of the ox, deer, sheep, horse, or the still more complex grinder of the elephant, first cuts through the gum, the crown is covered with a thick layer of cement, which dips in between folds of enamel, which, in their turn, conceal variously-disposed plates of dentine. In the course of time, the cement on the grinding surface is worn down, and the folds of the subjacent enamel

become visible. With further attrition, the cement between the folds of enamel wears away faster than the enamel itself, and hence the broad surface presents ridges corresponding with the harder enamel, and furrows corresponding with the softer cement, an arrangement well adapted, like the roughened surface of a mill-stone, for the grinding of hard grain, woody fibre, or roots. As the process of wear extends, the summits or bent parts of the folds of enamel are also worn through, and the concealed plate of dentine is exposed; in this case, the most complex markings appear on the grinding surface, produced by the alternating and often tortuous bands of dentine, enamel, and cement.

When the mammalian teeth, whether simple or complex, are worn down to the fang, they generally, as in Man, loosen and fall out; for their growth is completed at a certain period, after which their pulps shrink, they become subject to wear or decay, and undergo little or no repair. A remarkable provision exists, however, for the preservation of the cutting edge of the chisel-like incisor teeth, characteristic of, and necessary to, the *gnawing* Rodentia. These teeth show a persistent growth; the fang is deeply implanted in the jaw, and remains hollow and open at the base, into which the persistent pulp extends. The so-called enamel organ, on the anterior wall of the socket, is also persistent. Fresh dentine is constantly being formed within, upon the pulp, and fresh enamel upon the anterior surface, by the enamel organ; whilst the unequal wear of the hard coating of enamel in front, and of the dentine behind, preserves, during the whole of life, the chisel-like edge. From the persistent growth of these peculiar teeth, it happens, that if one of them be drawn or accidentally lost, the opposing tooth being no longer worn down by use, continues to elongate, and, following its natural curve, attains an abnormal size and shape, and its point turns round, and even penetrates the opposite lip. The teeth of the armadilloes and sloths also grow continuously, on persistent pulps.

In many Mammalia, sex exercises a remarkable influence on the development of certain teeth. Thus, in the Quadrumana, especially in the anthropoid apes, the upper canine teeth, in the male, are more than twice the size of the same teeth in the female; the tusks of the boar and of the male elephant, and musk-deer, are larger than those of the female animals. In the dugong, which, an exception in Cetacea, has both temporary and permanent incisor teeth in the two jaws, the upper permanent incisors project beyond the gum, in the male; but in the female, the permanent incisors in both jaws remain concealed throughout life, their growth being arrested before they cut the gum. The asymmetrical tusk, the rudimentary and, concealed condition of the opposite tooth of the male narwhal, and the hidden rudiments of both teeth in the female, already mentioned, also show the influence of sex.

This rudimentary condition of certain teeth is, however, sometimes independent of sex, but characterises groups of animals. Thus in the ox tribe, although the temporary incisors appear above the gum in both jaws, the permanent incisors are not developed in the upper jaw, but remain in a rudimentary condition within the bone.

The four canine teeth also exist, in a rudimentary state, in all young Ruminants, though they never rise above the gum. In both jaws of the young whale-bone whale, rudiments of teeth exist, which are never further developed.

Birds.—In *Birds*, the horny coating of the edentulous jaws, is developed, in successive laminae, from the tegumentary membrane covering those bones. In the parrots, this horny coat is thick, and is formed and supported upon papillae. The absence of teeth in birds, is associated with the existence of a muscular stomach, or gizzard.

Reptiles.—Of these animals, the Saurians exhibit the most perfect dentition, then the Ophidians, whilst the Chelonia are edentulous, their jaws being covered with a thick and dense horn, variously modelled, so as to act in bruising or dividing the food, the jaws of the vegetable feeders being thick, and those of the carnivorous species sharp on their edges.

In the Reptiles which possess teeth, the number varies, but in existing species, it is never very small, being 30 in certain monitor lizards, and 29, the lowest known number, in the Ophidian amphibia. The number is not so determinate, nor are individual teeth so specially characterised, as in the Mammalia. In the crocodiles, and in many lizards, the teeth are limited to the jaw-bones; but they exist also on the pterygoid bones in the roof of the mouth, in the iguana, and on the palatine and pterygoid bones, in most Ophidia. In many of the latter, teeth are absent from the inter-maxillary bones. The jaw-teeth form single arches, excepting only in the caecilia or blind-worm, in which the lower front teeth are arranged in a double row.

The typical form of the reptilian tooth is conical, but in a few species this is departed from. These conical teeth vary greatly in size from the minute teeth of the blind-worm, to the powerful canine-like teeth of the crocodile. They are sometimes cylindrical, but more frequently compressed, or much flattened and blade-like, having sharply trenchant, or even serrated, margins. The surface is either smooth and polished, or longitudinally striated. In the iguanas, the crowns of the teeth are widely expanded, and their sides and margins curiously notched. The teeth are relatively longest in Serpents, and in the case of the *poison-teeth* or *fangs*, present a remarkable structure. These *poison-fangs* are strongly recurved, and contain a canal, opening at both ends on the anterior or convex aspect of the tooth, above, close to the gum, and below, a short distance from the point of the tooth. The secretion of the poison-gland, found at the side of the head, is conveyed by a duct, to the opening of the poison-canal near the base of the tooth. Into this, the poison is forced by muscles which tighten the gland capsule and compress the gland; and thence it is conveyed, through the opening in front of the point of the tooth, into any wound. The poison-fangs are ankylosed, or fixed by osseous union, to the superior maxillary bones; but since, in the poisonous serpents, these bones are movable, the poison-teeth can either, as when at rest, lie flat upon the gum, or they can be brought into a vertical position, in the act of striking.

The teeth of Reptiles have a short undivided root, which is, for the most part, ankylosed to the bone on which it rests. In the crocodiles, however, the teeth are separate, and are lodged in deep sockets; in the black alligator, the front teeth are embedded in sockets, whilst the hinder ones are fitted into a continuous groove. In the serpents and geckos, the ankylosed teeth are fixed to the sides of shallow sockets, but in the chameleons and most lizards, to the inner surface of a single alveolar plate.

Reptilian teeth always contain dentine and cement, sometimes also enamel and true bone. In most Saurians, the enamel exists as a thin coating over the crowns. The presence in certain teeth, of bone, besides the cement covering the dentine, depends on the conversion of the base of the pulp into bone, as the tooth becomes ankylosed to the jaw. The microscopic structure of the dentine, differs slightly from that of the dentine in Mammalia, its substance being traversed by canals communicating with the pulp cavity. In the iguana, the dentine is singularly inflected on its surface. In the poison-fang of the serpent, the dentine is folded on itself, in front of the pulp-cavity, so as to form the poison-groove or canal; a longitudinal section of the tooth, shows the tapering pulp-cavity behind the poison-canal; whilst a transverse section shows this canal surrounded by the dentine, coalescing in front of it, the pulp-cavity forming a crescentic fissure behind it.

As the teeth of Reptiles wear out and fall away, an almost unlimited succession of new ones replaces them throughout life, a process entirely different from the simple succession of temporary and permanent teeth in the Mammalia. The new tooth usually appears at the inner side of the base of the old one; but the poison-fangs of the serpents are replaced by new teeth, formed behind the old ones.

When, as is usual, the teeth are ankylosed to the jaw, the new tooth simply grows up on a papilla, and replaces the falling one; but in the alligators and crocodiles, in which the teeth are lodged in sockets, the new tooth, also formed on a papilla, gains access, by a process of absorption, to the interior of the old one, penetrates its pulp, grows up within it, raises it, and finally throws it off from its own summit. By this time, as seen in the gavial, another rudimentary tooth is formed, and proceeds to grow, in like manner, into its predecessor. The process of absorption resembles that of the fangs of the milk teeth, in Mammalia; and like that, it has been incorrectly attributed to mechanical pressure; for the growing tooth is softer than the old one, which is being absorbed.

Amphibia.—Fine prehensile teeth are found on the upper jaw and palate bones of the frogs and salamanders, more seldom on the lower jaw also. In the toads, only palatal teeth are present. Teeth are absent in the proteus and siren.

Fishes.—The teeth of Fishes present extraordinary varieties, greater than those of any other Class. Their number is almost countless in the silurus, its allies, and in the pike; but they become fewer or wholly absent, in the lower orders of fishes. The chimærae have two teeth in the lower, and four in the upper jaw; the lepidosiren has only a single dental plate in each jaw, and two small teeth on the nasal bones; the tench has one tooth on the occiput, besides some on the pharyngeal bones; whilst the myxine and myxinoid fishes have a single tooth on the palate, meeting two dental plates upon the tongue. Lastly, in the syngnathus or pipe-fish, in the hippocampus, in the Lophobranchiate fishes, in the sturgeon, ammocete, and amphioxus, no teeth exist.

The shape of the teeth in fishes, differs much. They are usually simple and conical; they are minute, numerous, and *villiform* in the perch; longer, *ciliiform* or *setiform*, often bifid or trifid; and rasp-like or *raduliform*, on the back of the vomer in the pike. They are commonly cylindrical, but sometimes flattened into a lancet-like blade, either straight, curved, bent sideways, or even barbed. The base may be broad,

as in the larger teeth of the pike, the lophius, and certain sharks; the edge is sometimes finely serrated, as in the sharks generally, or is notched, so as to divide the tooth into from two to five lobes. In other less known fishes, they are short and blunt, cubical, or prismatic, with from four to six sides, and closely arranged in a sort of mosaic work, showing their convex or flattened summits over broad surfaces. These surfaces are well calculated for grinding seaweeds, and crushing shell-fish or corallines, as seen in the teeth of the scarus or wolf-fish, and the cuneiform dental plates of the parrot-fish, which truly masticate their food.

The teeth of Fishes, as already indicated, are by no means limited to the premaxillary and premandibular bones of the upper and lower jaws. In the sharks and rays, they are thus confined to the fore-part of the mouth; but in the carp, all the teeth are at the back of the mouth, supported on the pharyngeal and basi-occipital bones. The parrot-fish has teeth, both at the front and back of the mouth, *i.e.* on the premaxillary and premandibular bones, and on the upper and lower pharyngeals. In most fishes, there are teeth, not only on the above-named bones, but also on other bones around the middle part of the mouth, as on the palate bones, vomer, hyoid bones, and branchial arches, sometimes on the pterygoid, sphenoid and nasal bones, and, though rarely, on the true superior maxillæ. Teeth are found in the median line, on the palate of the myxines, and even, in a few cases, on the symphysis of the jaw, a position not observed in any other Vertebrata. In the lampreys, most of the teeth are placed on the lips.

The teeth of Fishes are usually anchylosed to the bone on which they rest, the dental and osseous tissues being blended; occasionally it is the side of the tooth, and not the base, which is thus fixed. In certain Cartilaginous fishes, some of the teeth are divided at their base, and are so attached by ligaments, as to allow the teeth to be bent backward in the mouth, by casual pressure; but when this is removed, the teeth spring up again. Even the anchylosed teeth are first attached by ligament only. A few examples are met with of the teeth being embedded in sockets; but then also ankylosis exists. The short strong teeth, which almost pave the mouth of the wolf-fish, are anchylosed to special eminences.

The teeth of Fishes are almost invariably composed of some kind of dentine only, the enamel and cement being absent. In certain cases, as in the carp, the tooth substance is brown and semi-transparent; in the Cyclostomata, it has been differently described as dense, albuminoid, or horny; the labial teeth of certain goniodonts and chætodonts are flexible and elastic. The true *dentine* of fishes' teeth, is very compact, especially on the surface of the tooth, where it occupies the place of enamel; this superficial layer has been called *vitro-dentine*. Another modification of dentine, commonly found in fishes' teeth, is named *osteo-dentine*, because it contains vascular canals, resembling the Haversian canals of bone, between which are dentinal tubuli, no longer minute and parallel, but large, divided, and ramified. The so-called *vaso-dentine* is also found in the teeth of fishes, and, though more rarely, the *plicio-dentine*, *labyrintho-dentine*, and *dendro-dentine*, so called from the *folded*, *wavy*, or *dendritic* appearances seen in them on sections. Although teeth consisting of dentine alone, are only found in fishes, yet the most complex known teeth are met with in this Class. Thus, in the wolf-

fishes, and diodonts, the teeth contain dentine, osteo-dentine, enamel, and cement; and in the parrot-fishes, each pharyngeal tooth is composed of non-vascular dentine, covered by an enamel, ankylosed to the bone by vaso- or osteo-dentine, and fixed to the neighbouring teeth, in the same row, by intermediate cement.

The teeth of Fishes, besides being liable to be accidentally torn off at their bases, are shed not merely once, as in Mammalia, but many times during life. In the pike and other common fishes, and in the Cartilaginous fishes, as the sharks, the formidable teeth are renewed and continually advance into place from behind, as the old ones break, or fall out. A few quite exceptional examples of strictly permanent teeth are met with, as in the lepidosiren and chimera.*

The Jaws and their Muscles.

The oral aperture of the Vertebrata, is a transverse opening, provided with jaws, one or both of which move *vertically*. In the Cyclostome fishes, the mouth, however, is *circular*; and, in the amphioxus, oval and longitudinal.

The form and strength of the jaws, the mode of articulation and motions of the lower jaw, or of both jaws, and the corresponding muscular apparatus, vary with the habits and food of the different Vertebrata.

In all the *Mammalia*, as in Man, the upper jaw is fixed to the bones above and behind it, and has no independent motion; whilst the lower jaw is movably articulated to the under side of the temporal bones, and is raised, moved horizontally, or depressed, by muscles exactly similar to those found in the human body.

In the large Carnivorous mammalia, however, the glenoid fossæ are not shallow, as in Man, but deep, narrow, and form long channels running from side to side, and inclining backwards and inwards towards each other. As the condyles of the lower jaw are equally narrow and elongated transversely, the motions of the jaw are limited to an up and down motion, in which not only is a general, firm hold secured, but the notched edges of the laterally compressed molars pass close by each other, like those of the blades of scissors. In Insectivorous mammalia the motions of the jaws are almost equally limited. In the Rodentia, besides shutting powerfully in gnawing, the jaw executes rapid backward and forward movements, *across* the ridges of their molar teeth, so as easily to grind tough vegetable substances. In the Herbivora, the lower jaw is not limited to an up and down movement only, as in the Carnivora, nor to that, and a superadded backward and forward movement, as in the Rodentia, but it is also capable of great lateral play. To permit this, the glenoid fossæ are wide and shallow, the condyles of the lower jaw are short, obtuse, and scarcely prominent, and the pterygoid muscles, which chiefly execute the lateral motions, are very large. The lower jaw is carried, during mastication, in a sort of circular sweep, beneath the upper jaw, first forward, and to one side, and then back-

* See the article 'Teeth,' by Professor Owen, Cyclop. Anat. and Phys., from which the preceding account of the teeth in the Vertebrata is chiefly derived.

ward and to the other, and so on, as may be readily noticed in the cow, when chewing the cud; the broad molar teeth, with their unequal ridges and furrows of enamel and cement, are thus most effectually employed. In the edentulous ant-eater and ornithorhynchus, the condyles of the jaws, and the glenoid fossæ, are only slightly developed, and the movements are comparatively simple and feeble.

In *Birds*, the actions of the jaws are prehensile and not masticatory, excepting perhaps in the parrots, in which there is a lateral motion. For the most part, the motion is hinge-like, and not very powerful, excepting in the strong-billed birds, such as the finches, rooks, toucans, and Raptores, which latter hold and tear their food by movements of the head and neck.

In *Reptiles*, whether they live on animal or vegetable food, the jaws are also prehensile, or incisive, rather than masticatory, except in the herbivorous iguanas, the molar teeth of which are large and tuberculated. In *Amphibia*, the jaws are weak, and snapping or suctional.

In *Fishes*, the movements of the jaws are, likewise, for the most part, simply of a snapping and prehensile or incisive character; but the pharyngeal and other dentigerous bones within the mouth, are also movable, and these bones, as well as the jaws, especially in the parrot- and wolf-fishes, are provided with strong masticating muscles, which make them act powerfully against each other.

Denticles of the Non-Vertebrate Animals.

As already stated, true teeth are found only in the Vertebrata, but denticular organs are met with in some of the other Sub-kingdoms. Amongst the Mollusca, the Cephalopods are provided with horny jaws, which open and shut vertically. Some Gasteropods, also, have similar, but smaller, jaws moving laterally; but nearly all of them are provided with a peculiar strap-shaped band, beset with rows of minute horny denticles situated in the mouth, and often spoken of as the *tongue*. This organ, named by Huxley the *odontophore*, is placed not on the floor, but on the roof, of the mouth. It is moved backwards and forwards by appropriate muscles, and thus files or rasps very hard substances; as its anterior part is worn away, the odontophore, with its horny denticles, is renewed within a special sac, seen at its hinder end.

Amongst the *Annulosa*, the Arthropoda have mandibles, always found at the sides of the mouth, and provided with strong muscles, which give them a *horizontal*, not a vertical motion; they are composed of calcareous or chitinous substance, and differ remarkably in shape, in different species, being usually curved and pointed, and having serrated or dentated edges; they are strong in the actively feeding larvæ, and also in most perfect Insects, as in wasps and beetles. In the Crustacea, the mandibles are very strong, and in certain species, as in the lobster, hard gastric tubercles, worked by powerful muscles, exist at the entrance of the stomach. Even amongst the soft Annelids, a denticular apparatus exists, as seen in the leech, which, by means of three minute denticles, inflicts a tri-radiate wound.

Amongst the *Annuloida*, many of the minute Rotifera possess complex denticulated plates, which are worked transversely across the oral orifice. In the hard-shelled Echinodermata, a singular masticatory apparatus

is found which, in its perfect form, consists of five large flattened, calcified denticles, having their free edges surrounding the oral aperture; the outer borders of these denticles, very peculiar in form, are received into a frame-work, the whole structure, in its entire state, forming the *lantern of Aristotle*; powerful muscles act upon these denticles, which comminute, or triturate, the food.

No denticles exist in the Cœlenterata; minute denticular organs are seen in some of the stomatode Infusoria, but they are, of course, absent in the astomatous Protozoa.

The Salivary Glands, and Insalivation, in Animals.

Salivary glands, or glands opening into the mouth, exist in most animals. In the Mammalia, they are nearly always present, but differ much in number and size. In the higher Mammalia, they resemble the glands in Man, except that the submaxillary is unusually large, and, in the seals and cats, the sublingual gland appears to be wanting. In Herbivorous, the salivary glands are larger than in Carnivorous Mammalia, in harmony with the more bulky, often drier, and amylaceous character of the food. In the Ruminants, all the glands, but especially the parotids, are very large, and even supernumerary glands are found, as in the ox. In the ant-eater, the salivary apparatus is enormously developed; the glands cover the fore-part of the neck, and, even reach to the chest; a special reservoir, or *salivary bladder*, exists beneath the mouth, in which the saliva is probably detained; when rendered viscid, by absorption of its fluid, it lubricates the tongue, and assists in catching ants. In the Cetacea generally, the salivary, like the lachrymal, glands are wanting, the fluid medium in which they live, and the animal nature of their diet, rendering saliva unnecessary; in the herbivorous dugong, however, the parotid glands exist, but not the sublingual.

In *Birds*, the salivary glands are small in the wading and web-footed species, which live upon soft animal food; whilst they are proportionally larger in the rapacious and granivorous species. The saliva of birds is chiefly used to lubricate their food. In the woodpeckers, these glands are large, and the viscid saliva assists the tongue in entangling insects. In the Chinese swallow, which builds the edible nests, the parotid gland is largely developed, and its secretion is used in making the nests.

Amongst *Reptiles*, large salivary or buccal glands, found in the Ophidia generally, but not in all species, beneath the gum, along the margins of both jaws, serve to lubricate their prey before it is swallowed. The poison-glands of the venomous species, may perhaps be regarded as extraordinarily modified salivary or buccal glands. In the Chelonian and Saurian reptiles, the salivary apparatus consists chiefly of lingual glands. In the chameleon these are found in the enlarged extremity of its singularly formed insect-catching tongue, and secrete the slimy mucus with which it is covered.

In the *Amphibia*, similar glands are found, which, in the toad, serve a like office.

In *Fishes*, no salivary glands exist.

In the *Mollusca*, glands opening into the mouth, or into the commencement of the gullet, and therefore presumably salivary, exist in nearly all

Cephalopods, Pteropods, and Gasteropods, varying in form and size, according to the construction of the mouth, and the nature of the food.

Amongst the *Annulosa*, glands, always regarded as salivary, exist in well-marked, but most variable forms, sometimes opening into the mouth, at the base of the mandibles, or beneath the proboscis, and sometimes further down, near the stomach. These glands are, of course, minute, and simple in structure, forming, either short follicles, vesicles, blunt-ended tubes, long twisted tubes, as in all butterflies, and most beetles, or even branched tubes, as in Blaps. In the Myriapods, similar glands exist. In the Cirrhopods, they are of considerable size, and form the cement gland.

In the Annuloid Echinodermata elongated cæcal tubes surround the œsophagus, and secrete a viscid fluid, which mixes with the food. Salivary tubuli have even been described in the Entozoa and Rotifera. No such glandular structures exist in the Cœlenterata, or Infusorial Protozoa.

The Pharynx and Gullet, and Deglutition in Animals.

The parts concerned in deglutition and the act itself, are similar in all the *air-breathing* Vertebrata, but both become gradually simplified. The uvula is absent, excepting in the higher Quadrumana. The soft palate is very large in the elephant and the Cetacea. Tonsils are always present. In all cases, from the highest Mammalia down to the Amphibia, the pharynx communicates with the cavities of the mouth, larynx, and œsophagus, and also, on each side, with the tympanum. In Mammalia, the structure of its walls resembles that in Man, and in the second stage of deglutition, it rapidly and safely transmits the food and drink into the œsophagus, over the laryngeal opening, whilst the third or œsophageal stage of deglutition is also, as in Man, performed more slowly by waves of peristaltic contraction, even against gravity, as is seen in the horse, when drinking. In *Birds* and *Reptiles*, the pharynx is of simpler construction and action, being in the Serpents enormously dilatable. In the *Amphibia*, it approaches the less defined character which it presents in Fishes.

In *Fishes*, which respire in the water, by gills, the pharynx has no communication with the nasal fossæ, and, moreover, the larynx and air-breathing apparatus are absent, except, in some cases, the air-bladder; hence the pharynx forms a mere infundibular passage, leading from the mouth into the shut œsophagus; but its sides are supported by the cartilaginous or bony framework of the branchial arches, between which are the branchial openings; besides this, there are special pharyngeal bones, which, as already mentioned, often bear prehensile or even masticatory teeth.

In the Molluscous, Annulose, and still lower Classes, a special pharynx is seldom distinguishable; but the buccal cavity usually passes directly into the œsophagus. In the Molluscoida, however, a part called the pharynx, exists between the mouth and the œsophagus.

A true pharynx is, indeed, characteristic of the Vertebrata, and is specially developed in those which respire air, and in which the food has to be swallowed, without entering the sensitive air-passages, and

with but a momentary interruption to the breath. In the cold-blooded Serpents, however, which swallow animals entire, deglutition is painfully slow, and causes a certain interference with respiration. In the young kangaroo, whilst it is still retained in the marsupium or abdominal pouch, the upper part of the larynx is elongated, and projects, as in the Cetacea, into the posterior nares, so that the milk passes down on each side, without risk of entering the air-passage, and without interference with the act of breathing.

The Stomach and Intestines in Animals.

Mammalia.—In the Quadrumana, the stomach often resembles that of Man, but it is sometimes globular or elongated, sacculated, constricted, or bent on itself; a cardiac and a pyloric portion are always recognisable. In the Carnivora, the stomach also presents the human shape, but the cardiac pouch is large. In the insectivorous Cheiroptera, it is globular; in the vampyres, it is long and conical, the cardiac end being the larger; in the frugivorous species it is still longer, the cardiac pouch is constricted in its middle, and the pyloric portion is bent. In the proper Insectivora, this organ is elongated. In the Edentata, it is usually simple; but in the genus *Manis*, the cardiac and pyloric portions are marked off by an internal fold, and, in one species, a long sac extends from the pyloric portion. In the sloths, the stomach is first divided into a cardiac pouch and a pyloric portion; the former has a dense epithelium, and is again subdivided into two parts, one ending in a blind canal; the pyloric portion has thick walls, and a soft mucous membrane, and is subdivided into two parts, which might be compared with the third and fourth stomachs of the Ruminants. In the anteaters, the cardiac part of the stomach constitutes a kind of *crop*, whilst a second chamber, having thick walls and a hard gristly lining, somewhat resembles the *gizzard* of the bird, and, compensating for the want of teeth, crushes the ants, by aid of the sand swallowed with them.

It is in the Ruminants, however, which are all vegetable-feeders, that the stomach presents the most remarkable complication, being divided into four distinct cavities; first, the *paunch*, *rumen*, *ingluvies*, or *panse*; secondly, the *honey-comb*, *water-bag*, *reticulum*, or *bonnet*; thirdly, the *omasum*, *manyplies*, *psalterium*, or *feuillet*; and, fourthly, the *abomasum*, *reed*, *rennet*, or *caillet*. The *first* stomach, or *paunch*, is the largest, sometimes attaining enormous dimensions; it forms a bag, constricted at one point, and placed to the left of the œsophagus, which opens into its right upper end; its mucous membrane is papillated, and covered with a dense white squamous epithelium. In the camel tribe, two clusters of diverticula, or cells, exist, one on each side of the paunch. In the dromedary, each cluster is eighteen inches long and six inches broad. The component cells, quadrangular, and arranged in rows, are, when distended, about three inches wide and deep; their orifices are closed by membrano-muscular folds; some are subdivided by membranous ridges into secondary cells. These *water-cells* of the paunch are intended for storing up water, which is found only at long distances in arid countries. They are emptied by the action of their muscular walls.

The *second* stomach, or *honey-comb*, much smaller than the paunch, forms a simple bag beneath the œsophagus, between the paunch and the

third stomach or manyplies. Along the inner surface of its upper concave border, is a peculiar *demi-canal* or groove, named the *œsophageal groove*, which runs from the *right* half of the œsophagus, of which it seems a continuation, on into the manyplies; its borders, composed of the muscular, submucous, and mucous coats, are much elevated, and can be brought together, so as to form a tube leading directly from the œsophagus, past the paunch and honey-comb, into the manyplies. The interior of the honey-comb is characterised by a cell-like or reticular structure, being developed into numerous polygonal cells, which are shallow in the reindeer and giraffe, deeper in the ox and sheep, and still more capacious in the llamas and camels. The mucous membrane, in the horned species, is papillated, especially on the inter-alveolar ridges. The cells of the honey-comb or water-bag retain water, which during digestion is mixed with the food. They are not proper water reservoirs, like the cells of the camel's paunch; for, unlike these, they have no marginal covering folds, are always open, are more sub-divided internally, and do not, when filled, bulge on the outer surface. Moreover, the cells of the honey-comb are present in all Ruminants, whilst those of the paunch exist only in the camels, dromedaries, and llamas.

The *third* stomach, or *manyplies*, is usually the smallest cavity of the complex ruminant stomach; but in the camels it is larger than the honey-comb. It forms a sac, placed between the honey-comb and the fourth stomach, or rennet-bag; it communicates with the former, by a narrow passage, but opens quite freely into the latter. Its inner surface is remarkably increased by numerous longitudinal laminae or folds, having their free edges turned towards the cavity, varying alternately in depth, and numbering from forty, in the sheep, to twice that number, in the ox; their resemblance to the leaves of a book, has given rise to the appellations manyplies, psalterium (psalter), and feuillet. The mucous membrane of the manyplies is villous.

The *fourth* stomach, or *rennet-bag*, from which, in the calf, the rennet is procured for curdling milk in the manufacture of cheese, is about one-third of the size of the paunch; it is elongated and conical in form, being wider at the left end next to the manyplies, and gradually narrowing towards the pylorus, near which the muscular coat is thickened, and where a circular pyloric valve exists. The mucous membrane, thrown into loose, irregular, longitudinal rugæ, connected by smaller transverse ones, is soft, destitute of villi, and highly vascular. It is chiefly composed of the countless gastric follicles, which open upon its surface. The rennet-bag is the true digestive stomach, being the only part of the compound ruminant stomach which secretes gastric juice.

The ruminant animal, cropping its herbaceous food, first partially masticates and insalivates it, and then swallows it. Afterwards, the animal being at rest, the food, so swallowed, is returned into the mouth, where it is *now* remasticated and once more swallowed. This constitutes the act of *rumination*, characteristic of these animals. The crude food, when first swallowed, descends in largish masses, which force open the borders of the œsophageal groove, and so escape into the paunch. Water, doubtless, is conducted along that groove into the honey-comb, or so-called water-bag, but it also partly escapes between the margins of the groove, and so enters the paunch, where, in the camel tribe, it is received into the system of water-cells there situated.

The food, partially masticated and insalivated, lubricated with mucus, and mixed with water and the juices of the paunch, undergoes maceration in that cavity, and also probably enters the honey-comb, in which it is further watered. Now, moulded by muscular action into small masses or pellets, either in the cells of the honey-comb bag, or by the œsophageal groove itself, it is propelled into the œsophagus, and thence, by an anti-peristaltic action, into the mouth. The soft and small pellet is there deliberately remasticated and insalivated, and is thus reduced to a semi-fluid pulp, which again passes down the œsophagus, and the margins of the œsophageal groove being now closed by muscular contraction, so as to form a complete tube, the semi-fluid mass is this time transmitted into the third stomach, or manyplies, from which it cannot return. Here it is brought into contact with a large surface of mucous membrane, loses much fluid and soluble saccharine and other substances, and is then passed on to the rennet-bag, for the digestion of the albuminoid matters.

The precise mode of action of the borders of the œsophageal groove and other parts, is not known. Some suppose that the animal conveys the food or drink, instinctively or voluntarily, either into the first or second stomach, or else into the third. But according to another view, the process is partly a reflex act, and partly mechanical. In every act of deglutition, the borders of the œsophageal groove are believed to be approximated by a co-ordinated muscular act. When the food or fluid swallowed, is large in mass or quantity, it is supposed to overcome the muscular action, and so to pass, if solid, into the paunch, and, if fluid, partly also into the honey-comb; but if the material swallowed be semi-fluid or fluid, and in moderate quantity, it is suggested that it may be conveyed along the temporary tube into the manyplies (Flourens). In the act of sucking, the milk is said to pass at once into this cavity, on account of the small quantity swallowed at a time. It is not certain whether the regurgitated pellets are moulded in the cells of the honey-comb bag itself, or in the œsophageal groove; nor whether the pellet is introduced into the lower end of the œsophagus, by the contraction of the sides of the groove, or by that of the reticulum itself. Though reflex, and probably excited by the food as a stimulus, and therefore not volitional, these movements of the ruminant stomach and œsophagus may be in some extent controllable by the will.

In the Pachydermata, the stomach is more simple. Thus, it is elongated, and possesses a long cardiac pouch in the elephant and rhinoceros, but in the former, it presents numerous internal transverse folds. The hippopotamus has two cardiac pouches, opening widely into the rest of the stomach; in the tapir and hyrax, this organ forms two cavities. In the pig, the stomach resembles externally that of Man, though the cardiac end is more projecting, and a considerable extent of the lining membrane, near the œsophageal opening, is covered with a thick epithelium. In the peccary, still more of the cardiac portion is lined by a dense epithelium.

In the Solipeds, the stomach is rounder, the œsophageal and pyloric openings are near to each other, and the cardiac portion of the organ is lined by a thick epithelium, which terminates by a dentated margin.

In the Rodentia, the stomach is also marked off into a cardiac and pyloric portion, often indicated by an external constriction; the cardiac

part is lined by a thick epithelium, and the pyloric end by a soft glandular mucous membrane. In the beavers, and some other species, the stomach has glandular crypts and cæca, the use of which is not known.

The Marsupials, whether carnivorous or herbivorous, have usually a simple somewhat elongated stomach, sometimes provided, like that of the beaver, with numerous crypts. In the kangaroo, the stomach is of remarkable length, being as long as the body; its middle portion is sacculated, and marked by three longitudinal muscular bands, somewhat like the colon; it has three compartments, two being cardiac pouches, and also three rows of large crypts along the bands.

It is remarkable that the carnivorous Cetacea have a more complex stomach than the herbivorous species. In the dugong, amongst the latter, this organ is elongated, and marked off into a cardiac and a pyloric portion, by a constriction, from near which two blind pouches proceed; the cardiac pouch presents a large glandular surface. The carnivorous cetacean stomach possesses from three to seven cavities, the first of which has a thicker epithelium than the rest.

On taking a general view of the above described modifications of the mammalian stomach, it would seem that, in its simplest form, it is a specially dilated part of the alimentary canal, distinguished by its abundant glandular tubules; this becomes elongated and narrower at a certain part, next constricted, and then partially subdivided within, by internal folds. These subdivisions in the complex stomach become still more pronounced, and associated with important differences of structure in the various coats, especially in the lining membrane. The pyloric portion of even the simplest stomach has larger gastric glands than the cardiac portion; and, in the compound stomachs, this part alone presents gastric tubuli, and secretes gastric juice. The cardiac end, variously subdivided and modified, is often lined by a thicker epithelium, and has been regarded as a dilatation of the œsophagus.

The *intestinal canal* is, in all *Mammalia*, marked off from the stomach, by a circular muscular rim or pyloric valve. It presents even greater varieties than the gastric cavity, and these are more immediately referable to the nature of the food.

The most noticeable difference is in the relative length of the *intestines*, from the pylorus downwards, which are nearly always shorter in the flesh-feeding, and longer in the vegetable-feeding species, in every Order. The following Table illustrates both the rule and the exceptions:—

Flesh-Feeders.		Vegetable-Feeders.	
Carnivora—		Ruminantia—	
Cat, dog . . .	5 to 1	Sheep . . .	30 to 1
Bear, hyæna . .	9 or 8 to 1	Solipeds—	
Seal . . .	15 to 1	Horse . . .	20 or 15 to 1
Insectivora . .	6 or 3 to 1	Cheiroptera—	
Cheiroptera—		Frugivorous pteropus	7 to 1
Insectivorous bats . .	2 to 1	Quadrumana—	
		Omnivorous . . .	8 or 3 to 1

Excepting in the Cetacea, and a few Edentata and Cheiroptera, the subdivision into a small and large intestine, prevails throughout. According to its length, the small intestine is more or less convoluted; it usually has internal valvulæ conniventes, and a villous mucous mem-

brane; villi are always wanting in the large intestine. At the junction of the small with the large intestine, a more or less perfect ileo-cæcal valve is found, except in the Monotremata, Cetacea, and certain Edentata and Cheiroptera.

The colon is usually sacculated. A cæcum nearly always exists, its presence and size corresponding closely with the nature of the food, being either absent or small in flesh-feeders, and highly developed in vegetable-feeders. It is absent in all Insectivora and Cheiroptera, in some of the Edentata, and in certain Cetacea. In the Carnivora, generally, it is short and narrow, and is absent in the bears and weazels. It is present, and of variable length, in the Quadrumana. In all Ruminants, it is capacious, but it is still larger in the Solipeds, being, in the horse, three times as large as the stomach, and measuring two feet in length. In the Pachyderms, it is somewhat smaller, but the hyrax has two cæca. Amongst the Rodentia, the cæcum is absent in the insectivorous dormouse, short and small in the omnivorous rat; but it attains its greatest size, and is even marked by circular or spiral folds, in the herbivorous genera, as in the rabbit and hare, being, in the latter, eight times as capacious as the stomach. In the carnivorous Cetacea, there is usually no cæcum, but the balæna has a small one; in the herbivorous species, this part exists, being sometimes very large, but sometimes short and bifid. The carnivorous Marsupials have no cæcum, and the insectivorous species a small one; in the frugivorous species, it is wide, and twice as long as the body, and in the herbivorous species three times as long.

The narrow part of the cæcum, the vermiform appendix, present in Man, exists in the apes and gibbons, and in the marsupial wombat, but in no other mammalian animal.

In the Monotremata, a small cæcum alone indicates the place of junction of the small and large intestine; the intestinal canal is narrow, but widens below, and ends in a cloaca, as in birds.

Birds.—The digestive canal in Birds is usually complex, the œsophagus being more or less dilated near its lower end, to form the *crop*, or *ingluvies*, to which succeeds the *proventriculus*, or proper secreting stomach, and beyond this, is a third cavity, forming the *gizzard*. In the pelican, the floor of the mouth, and in some other birds, the sides of the fauces, are dilated into receptacles for food.

The *œsophagus* varies in length according to that of the neck. In the storks, herons, and pelicans, which swallow their prey whole, it is very wide, and in the cormorant, it forms a large pouch. It communicates freely with the proventriculus, and its longitudinally plicated mucous membrane has numerous follicles, which secrete a mucus to moisten the food, and aid in deglutition. The *crop*, or dilated portion of the œsophagus, is not distinct in the toucans and hornbills, or in frugivorous and insectivorous birds, or in most of the waders. It is even wanting, amongst the swimming birds, in the swans and geese, but is small in the ducks. The large birds of prey have a small crop, lodged in front of the furcular bone or merrythought, at the root of the neck. The crop is most developed in the grain-eating gallinacea, forming a dependent bag, connected with one side of the œsophagus, as in the fowl, or, as in the pigeons, consisting even of two lateral oval sacs. Where a crop exists, the short portion of the œsophagus below it, is named the second or

lower œsophagus; it gradually dilates into the proventriculus, which has no constricted cardiac orifice.

The *proventriculus*, also called the *ventriculus succenturiatus*, the true glandular stomach, varies in form and size in different birds, being sometimes wide and straight, and sometimes round. In the rasorial birds, it is wider than the œsophagus, but smaller than the gizzard; in the birds of prey, it is about the same size as the gizzard; in the parrots and storks, it is larger than the gizzard, and in the ostrich, four or five times as large. Its mucous membrane is thicker and more vascular than that of the œsophagus or even of the crop, and, as in the mammalian stomach, is provided with numerous gastric glands arranged perpendicularly to the surface, sometimes simply tubular, as in the carnivorous eagle and sea-gull, the insectivorous swallow, and the granivorous pigeon, and often sacculated, or even expanded into compound follicles, as in other grain-eaters, viz. the fowl, turkey, rhea, and ostrich. The disposition of these glands on the interior of the proventriculus, differs in different Orders, and even in different genera of the same Order. Thus, they may be diffused over the whole surface, or may form a single oval, elongated, or triangular cluster, two oval lateral clusters, or four arranged in a circular manner, or they may form a zone or belt.

The *gizzard*, *gigerium* or *ventriculus bulbosus*, the third, last, or *muscular stomach* of birds, is a more or less flattened, ovoid receptacle, having two neighbouring apertures at its upper part; one, into which the proventriculus opens, and the other leading into the intestine. Between and below, as it were, these apertures, the gizzard forms a cul-de-sac, varying in size, and having walls of variable thickness in different species. In the birds of prey, the muscular coat is thin, and its fibres radiate from two lateral tendinous centres. It is in the rasorial and flat-billed swimming birds, as exemplified in the fowl and swan, that the gizzard is most developed; the deep red muscular fibres here form four very thick masses, two of which, named the *musculi laterales*, constitute the sides of the gizzard, whilst two smaller ones, the *musculi intermedii*, are placed at one end; they all radiate from, and towards, two very strong anterior and posterior tendons. The cavity of the gizzard is comparatively small, and is bounded by two flat surfaces, covered by a very thick, cuticular, horny, or even tuberculated lining membrane, supported on a dense, fibrous, submucous coat. The lining membrane is hardest in the granivorous birds, especially in those species in which the food is most solid; its density increases at the points where the pressure and friction are greatest. In the petrel, it presents a layer of small square tubercles, suggesting a likeness to the gastric denticles of certain Gasteropods. Hunter observed that in a sea-gull fed on barley, the muscles and cuticle of the gizzard became thicker than natural.

A pyloric valve usually exists in Birds; it is placed, in most species, a little below the gizzard, so that there is a short pyloric portion of the stomach intervening between the gizzard and the duodenum. The pyloric valve is very strong in some birds; it is double in the gannet, and, in the ostrich, forms six or seven ridges, which close the pylorus like a grating, permitting only small stones to pass.

The uses of the crop, proventriculus, and gizzard of Birds, are obvious. The crop, absent or small in birds living on fruit, insects, small aquatic animals, or flesh, but reaching its utmost development in those which

feed on grain and other seeds, forms, like the ruminant paunch, a cavity for the retention and maceration, during several hours, of hard and dry food, so as to prepare it for the solvent action of the proper gastric juice of the proventriculus, and the grinding force of the gizzard. Seeds soften and swell under the influence of the scanty saliva, and of the more copious secretion of the crop. Pigeons will sometimes devour so many dry peas, as to be almost suffocated when these swell in the crop. The crop has been compared to the hopper of a mill, and the gizzard to the millstones, the former and larger cavity receiving the food, and delivering it, in successive suitable quantities, into the latter, which is so much smaller. Whilst rearing its young, the mucous membrane of the double crop of the pigeon becomes thicker and more vascular, its glands enlarge, and secrete a milky looking fluid, which mixes with the softened grain in the crop, and is then, by an antiperistaltic action, regurgitated into the mouth, from which, in the manner above-described (p. 118), it is taken by the young pigeon, serving the same purpose as the lacteal secretion of the Mammalia. The proventriculus of Birds has been compared with the cardiac, and the gizzard, with the pyloric, portion of the mammalian stomach. The secretion of the proventriculus has the same digestive properties as those of the gastric juice of Mammalia. The gizzard, which, when it exists, forms an internal masticatory organ, supplying the want of a masticatory apparatus in the head, has evidently a mechanical office. By the aid of pebbles, gravel, or sand, swallowed especially by granivorous birds, it triturates the food. Such birds do not thrive, without a supply of pebbles or gravel; and pigeons have been known to carry these to their young. Grains of barley, enclosed in strong perforated tubes, pass through the alimentary canal of the bird undigested, whilst meat, similarly enclosed, is dissolved. Unbruised corn, with its hard silicious coat unbroken, is not soluble in gastric or intestinal juice. The gizzard of the ostrich can flatten metal tubes, pulverise glass balls, and break or blunt the points of needles and lancets, without injury to its hard internal coat. The grinding of the stones in a bird's gizzard, may be heard by the stethoscope. The movements of the walls of this cavity, are supposed to be slightly rotatory. In the membranous gizzard of the cuckoo, as I, as well as others, have found, the hairs of caterpillars are sometimes impacted in a regular spiral manner, as if felted by a continuous movement of partial rotation; balls of hairs spirally disposed have also been seen. These facts have been often quoted, in support of the view that, in all animals, intrinsic movements of the walls of the stomach may occur.

The intestine of Birds generally, is, relatively to the body, shorter than that of Mammalia, but longer than that of Reptiles. It varies in length and width, as well as in the arrangement of the convolutions, and in the relative development of the cæca. In the birds of prey generally, the intestine is not more than twice as long as the body, including the bill, but in the osprey it is eight times as long. It is longer in frugivorous and granivorous birds, and shorter in the flesh-eating species. The duodenum always forms a long loop, embracing the pancreas. The remaining portion of the small intestine, is variously folded in different birds, the convolutions being either spiral, concentric, or irregular. The mucous membrane is usually plicated. The distinction between small and large intestine now becomes less marked, there being no ileo-cæcal valve, and

villi being found on the mucous membrane of both. Their place of junction is, however, frequently indicated by the presence of a cæcum, or rather of two cæca, for this diverticulum is most commonly double. The cæca are wanting in some vultures, in the cormorant, wryneck, and toucan, and in many carnivorous, insectivorous, and frugivorous birds; they are small and short in other vultures, in the eagles, and in the solan-geese, and also, when they exist, in the Insessorial tribes. They are longer in the nocturnal than in the diurnal birds of prey. Amongst the Rasores, they are short in the pigeons, but very long in the grouse, each measuring three feet, or thrice the length of the body, their internal surface being increased by eight longitudinal folds; in other Rasores, they are of moderate length. In the Cursorial birds, the intestinal canal, as well as other parts, approaches more nearly the mammalian character. The cæca, however, are absent in the cassowary, which obtains a constant supply of succulent vegetable food; whilst in the ostrich, which lives upon dry and scarce food, they are wide, about two feet long, and have an internal spiral fold, like that of the hare. In Birds generally, as in Mammalia, the cæca are absent, or small, when the food is concentrated and easily digestible; but when it is slower of digestion, or is taken in larger quantity, and at longer intervals, these appendages are most developed.

The large intestine beyond the cæca, is long and mammalian-like in the ostrich, but usually is relatively short, straight, and not very wide; it terminates by an imperfectly valved circular opening in the dilated cavity called the cloaca, into which also the ureters and the duct or ducts of the reproductive organs, open. In the hinder wall of the cloaca, is situated the glandular organ known as the *bursa Fabricii*.

Lastly, there exists in many birds a short, narrow, blind diverticulum, connected with the *small* intestine; this is the vestige of the *vitelline duct*, which, in the embryo and young bird, connects the yolk sac with the intestine. It is called the *vitelline cæcum*; it has no special digestive function. A similar diverticulum is occasionally found in Mammalia, and even in Man.

Reptiles.—The alimentary canal in this Class, is more simple than in Birds, to which, however, it approaches more nearly than to that of Fishes. The œsophagus varies in length, according to that of the neck; it is wide, plicated, and dilatable in the Ophidia; as in Birds, it joins the stomach without any constriction or cardiac orifice; but the mucous membrane suddenly ceases to have a dense epithelium, and becomes soft, smooth, and glandular. In the larger Saurians, the first part of the stomach has the form and structure of a gizzard, presenting thick muscular walls, the fibres of which radiate from two opposite central tendons; the pyloric part, more decidedly glandular, corresponds with the short portion sometimes found between the gizzard and the duodenum in Birds. In the Serpents, the cardiac part of the stomach is long, slightly saccular, and highly dilatable, whilst the pyloric portion is narrower and very muscular, being the only part like a gizzard. In the Chelonians, the stomach is curved, and larger at the cardiac than at the pyloric end. The pyloric valve is usually present in Reptiles, though not very distinct, and sometimes is scarcely recognisable.

The intestine in Reptiles is shorter and wider than in Birds. In the Saurians, there is mostly an ileo-colic valve; the crocodiles have no

cæcum. In the Chelonians, the intestine is long and muscular; an ileo-cæcal valve usually exists, and also frequently a cæcum. In Serpents, the small intestine especially, is elongated; the ileo-colic valve is indistinct, or its place is indicated only by a change in the size of the canal; the large intestine sometimes has transverse folds in its interior, analogous with the spiral valve in the same part in Cartilaginous fishes. As shown by the form of certain reptilian *coprolites*, these folds must have been well developed in some extinct Saurians. The mucous membrane of the large, as well as of the small, intestine is plicated and villous. The lower end of the larger intestine forms a cloaca, receiving the ducts of the urinary and reproductive organs. The presence of a cæcum in certain Chelonians, furnishes an additional example of the association of this organ with the use of a vegetable diet. The existence of a gizzard in some Reptiles, is one of the indications of the relations of this Class with Birds.

Amphibia.—The œsophagus of the Amphibia is short, dilatable and muscular. The stomach is fish-like, being tubular, wider at the cardiac than at the pyloric end, and placed transversely, or curved upon itself. The intestine in the toad and frog, is readily distinguishable into small and large, the former opening into the side of the latter; the ileo-cæcal valve is indistinct or absent. In the more fish-like Batrachia, the division into small and large intestine, is imperceptible. The latter ends in a cloaca, which receives the ducts of the urinary and reproductive organs. The relation between the length of the intestinal canal and the nature of the food, is illustrated in the long and coiled intestine of the young vegetable-feeding tadpole, as compared with the short intestine of the insectivorous adult frog and toad.

Fishes.—In Fishes, the alimentary canal presents its most simple vertebrate form, being wide, and, in relation to the body, short. The œsophagus, short, wide, and muscular, sometimes passes so evenly into the stomach that the structure of the mucous membrane alone distinguishes them; in the former, it is pale and longitudinally plicated; in the latter, it is softer, redder, and full of gastric tubuli. In the Cyclostomata, it forms only a dilated portion of the nearly straight canal. In the Osseous fishes especially, it varies in size, but is usually tubular, bent once upon itself, and narrower towards the pylorus; sometimes, by protrusion of the convex border, and shortening of the concave border, it becomes flask-shaped or globular, with its cardiac and pyloric openings placed near together. The cardiac orifice, large, and sometimes provided with a valvular fold, not only readily permits the swallowing of the prey whole, but sometimes allows of regurgitation and rumination, the food being remasticated by the teeth, or by the pharyngeal bones, as seen in the carp. The pyloric part is sometimes so muscular as to resemble an imperfectly developed gizzard, having thick walls and a dense squamous epithelial lining. A pyloric valve nearly always exists.

The intestine is relatively short and wide, of nearly uniform diameter throughout, has few convolutions, and is distinguished into a large and small intestine, by a slight constriction only; there is no distinct ileo-colic valve, but sometimes a short cæcum exists. The small intestine has usually connected with it, immediately below the pylorus, the so-called *appendices pyloricæ*, which have been compared with the pancreas. The large intestine is often, as in the sharks, provided with internal folds

or a spiral valve, by which its surface is much increased. It is also generally thrown into rugæ, which augment its surface. In some species, the intestine is unusually long; it is rarely supported upon a mesentery, excepting at a few points. The peritoneal cavity presents the unusual condition of opening directly on the exterior. In the singular amphioxus, the alimentary canal is short and nearly straight, the stomach being scarcely dilated; the intestine, as well as the mouth and sides of the pharynx, is provided throughout with cilia, which assist in moving on the fluids in the alimentary canal.

Mollusca.—In these animals, the alimentary canal, though simpler than in the Vertebrata, presents, as in them, many gradations, from a very complex form in the Cephalopods, to that of a slightly convoluted canal, with a simple dilatation for the stomach in the Lamellibranchiata. No distinction exists into small and large intestine.

In the Cephalopods, the œsophagus, which perforates the cephalic cartilage, is long, very dilatable, and ends in a strong gizzard, roundish or elongated in shape, lined with a hard epithelium, provided with two digastric muscles radiating from two lateral tendons, and having its cardiac and pyloric orifices near together. Sometimes, before entering the gizzard, the œsophagus expands into a crop. Below the pylorus, the intestine dilates to form a spherical, triangular, elongated, or spiral cavity, having a follicular mucous membrane; this has also been regarded as a stomach, but the ducts of the liver enter it through a sort of sac. Lower down, the intestine forms a simple, more or less curved, tube, which bends up, and opens into the branchial chamber, at the base of the mantle, not far from the mouth. The *ink-bag* is situated close to the lower portion of the intestine, and opens near it.

In the Pteropods, there are also, sometimes, found a crop and a distinct gizzard; the intestine presents three or four bends, surrounded by the liver.

In the Pulmo- and Branchio-gasteropods, the œsophagus is long, and frequently expands into a crop; the stomach itself often consists of two or more cavities; the first is usually lined with a thick epithelium, and is sometimes provided with hard internal laminae or denticles, constituting a sort of gizzard, which is most developed when the buccal masticating organs are least so; the second has softer walls, and forms the true digestive stomach. The relative position of these tritulating and digestive cavities, is the reverse of that met with in birds. The intestine, more or less coiled, larger and more tortuous in the vegetable-feeders, and usually embedded in the liver, receives the hepatic ducts, bends once or twice, turns forwards, and ends near the fore part of the body, usually on the right side, but sometimes on the left, or even on the back. It is lined with a ciliated epithelium.

In the Lamellibranchiata, the transverse mouth is concealed in the mantle, the œsophagus is short, the stomach forms a simple dilatation, and the intestine is relatively simple, describing a few turns, and ending by a straight portion, opening at the hinder part of the mantle; its convolutions are embedded in the substance of the liver, and its terminal part is sometimes embraced by, or perforates, the heart. As already stated (Vol. I. p. 127), the direction of the principal bend of the intestine, whether to the dorsal or hæmal, or to the ventral or neural surface of the body, is characteristic in each Molluscan Class (Huxley).

Molluscoida.—In the Ascidioida and Brachiopoda, the alimentary canal is very simple, consisting either of a convoluted, or of a short re-curved tube, merely dilated at the stomach, and having its terminal orifice approximated more or less, to the often wide and valved mouth. In the Salpida, the outlet of the intestine is at the hinder end of the body. In some Brachiopoda, the intestine ends in a blind-sac, having no inferior aperture or outlet.

In the Polyzoa, the mouth, situated in the centre of the circlet of ciliated tentacles, leads into a wide pharynx, and short œsophagus, which terminates in a muscular stomach; from this, the intestine bends upwards again, and opens near the side of the œsophagus, close to the outer border of the tentacular circle. In some species, the stomach is muscular or gizzard-like. These creatures present one of the lowest types of animals possessed of a true alimentary canal, distinct from the walls of the body, shut off from the peri-visceral cavity, and having a distinct and permanent inlet and outlet.

Annulosa.—The alimentary canal here also presents marked degrees of complexity, from the highly developed apparatus found in certain Insects, to the simple straight tube seen in the lowest Worms. The oral aperture or mouth, and the anal aperture or outlet, are always at opposite ends of the body. As a rule, the carnivorous kinds have a short intestine, and the vegetable-feeders a longer and even tortuous intestinal canal.

In the Insects, the alimentary canal varies with the stage of metamorphosis. In the vermiform larva, it is a straight tube, passing from one end of the body to the other; sooner or later, a dilatation appears, forming the stomach, which sometimes becomes divided transversely, and the œsophagus may also be further dilated into an ingluvies or crop. The intestinal canal presents cæca, and therefore a sort of distinction into small and large intestine. In the mandibulate Insects, as in the wasps and beetles, the crop is often glandular; the gizzard, which, unlike what occurs in Birds, is placed above the digesting stomach, has very muscular walls and a chitinous lining membrane, provided frequently with projections, laminae, hairs, or denticles, but sometimes this part is indicated only by being a little more muscular. The true stomach has soft delicate walls, usually provided with numerous gastric follicles. Sometimes the stomach has no follicles, but its interior is laminated, or developed into cells, or into a few short cæcal tubes; sometimes it is quite smooth. The intestine is generally narrow, more or less convoluted, and seldom supported by a mesentery, but rather by the tracheæ; it sometimes presents dilatations or divisions, so as to imitate, perhaps in form only, the subdivision into a small and large intestine. Certain fine cæcal tubes communicating with it, are probably glandular structures rather than diverticula of the intestine. The first part is undoubtedly fitted for absorption, whilst the lower end is more excretory. It presents a terminal dilatation or cloaca, into which the reproductive organs open.

In the Myriapods, the alimentary canal is narrow and nearly straight, and is either, as in the carnivorous species, merely slightly dilated, to form a stomach, or, as in the vegetable-feeders, complicated by pairs of saccular projections, which have been regarded as crops, or gizzards, but may be merely glandular recesses. The intestine is straight, wide,

plicated, and sometimes sacculated. Cæcal tubuli open into various parts of the alimentary canal.

In the Arachnida, the digestive tube is straight, very short, and comparatively simple. The stomach, scarcely dilated, has sometimes four appended sacculi, and sometimes cæcal prolongations, reaching into the bases of the palpi and legs. The intestine sometimes presents a globular dilatation, before it finally narrows.

Amongst the Crustacea, the higher forms, such as crabs and lobsters, possess a short wide sac, provided with internal hard calcareous, or chitinous denticles, which serve at once the purpose of a gullet, a masticatory apparatus, a stomach, and a gizzard. The denticles, arranged symmetrically around the canal, are worked by powerful muscles, and are shed when the animal changes its shell; besides the larger denticles, there are often stiff hairs, bristles, and horny ridges. The intestine, marked off by a constriction from this denticulated stomach, is short, nearly straight, and simple; it is sometimes subdivided by an imperfect valve, and, though seldom, has one or two cæca. In the lower parasitic Crustaceans, the alimentary canal is, however, straight and simple, becoming narrower as it passes backwards.

The shortness and simplicity of the alimentary canal, in the Spiders, Scorpions, and Crustacea, which live, some upon the juices of other animals, and some on crushed animal food, compared with the length and complexity of the digestive tube in vegetable-eating insect larvæ, or in the perfect beetles, further illustrates the modifications already noticed in the digestive canal of the higher animals, according to the nature of their food.

In the Annelida, the alimentary canal never presents any convolutions or bendings, and the mouth and outlet are always at opposite ends of the body. It has no mesentery. It is either quite simple, not even presenting a gastric dilatation, as in the lower marine species, or it is developed into simple tubuli, or subdivided pouches, or it may be regularly sacculated, as in the leeches, the blood sucked by those animals being retained, and slowly digested in the sacs. In the earth-worm, these sacs are represented by simple constrictions; it also has a sort of gizzard, and, within the intestine, a tubular cæcal organ, named the *typhlosole*, the use of which is not known.

Annuloida.—In the Rotiferous animalcules, the alimentary canal presents a pharyngeal dilatation, or crop, sometimes regarded as the stomach; the intestine is narrow and simple, opening sometimes at once on the surface, sometimes after forming a sort of cloaca; the orifice is usually near the hinder end of the body, on its dorsal aspect. In the Turbellaria, minute marine and fresh-water worms, an alimentary canal is present, which is either simple, sacculated, or most remarkably ramified or dendritic; with few exceptions, such as the Nemertis and Microstoma, it has but one aperture, viz. a mouth, which is often provided with a disc-like sucker, for holding on to surfaces; the pharynx also has a proboscis, for sucking or boring purposes. Of the parasitic Scolecida, the Nematoida, or thread-worms, have an alimentary canal, with both inlet and outlet, a pharyngeal dilatation, and a simple intestinal tube, sometimes, however, dilated, so as to form a sort of stomach, and sometimes a second dilatation lower down. In the Trematoda or flukes, such as the distoma, tristoma, and others, there exists either a double

or a ramified canal, with a common pharynx, but no anal aperture. In the Gordiacea, or hair-worms, there is likewise no such outlet. The organisation of all parasites, to whatever class they belong, is more or less aberrant.

In the Taniada or tape-worms, and in the Acanthocephala, represented by the echinorhynchus and echinococcus, also parasites living in the interior of other animals, there is no alimentary canal, nutriment being absorbed by them directly, through the integuments, from the digested food, or from the juices of the animal in which they live. In the tape-worms, straight tubes, with transverse or even radiating branches, exist, which are doubtless concerned in the nutritive processes, rather as circulatory and respiratory, than as digestive organs.

In the Echinodermata, the alimentary canal is well developed, distinct from the walls of the body, provided, in most cases, with openings at both extremities, and even supported by a mesenteric fold. In the Crinoida, the stomach and intestine are situated in the central part of the body, the latter opening at one side. Below the complex masticatory apparatus, elsewhere described (p. 128), the intestine of the Echinida, at first narrow, widens out, and presents a cæcal dilatation, beyond which the intestine coils twice round within the shell, reversing its direction in the latter half. In the Star-fishes, and also in the Ophiurida, the alimentary canal is very short, and gives off two ramified diverticula into each ray; the intestine opens by a minute orifice on the back; undigested matters are frequently discharged by the mouth. In the holothurida, the intestine describes a zig-zag course; the outlet is placed at the hinder end of the body.

Cœlenterata.—In this well defined aquatic Sub-kingdom, there is no longer an alimentary canal, separate from the walls of the body, and provided with an oral and anal aperture. The digestive canal is very short and wide, and has but one external opening, the mouth, which, however, serves both for the ingestion of food, and the egestion of residual matters, and excretions; at its inner end, the digestive canal opens widely into the general cavity of the body. From this latter, numerous canaliculi are prolonged, in the medusæ, into the disc, some of them opening by pores in its margins. In certain ctenophorous forms, as in *Beroë*, *Cydiape*, and *Cæstum*, the body cavity also opens, by one or two orifices or pores, at a point opposite to the oral aperture, but these are not intestinal or anal openings.

In the Actinozoa, the digestive canal projects a certain distance into the body cavity, which forms, outside that canal, the *perivisceral cavity*. In the Hydrozoa, the digestive canal becomes continuous, by a very wide opening, with the body cavity, without any portion of it projecting into that chamber; hence there is no surrounding or perivisceral chamber, and the outer surface of the continuous digestive and body cavities, are both in contact with the water. The hydra may be inverted, like the finger of a glove, and its outer surface, now become internal, will digest its food equally well.

In the compound Hydrozoa, the lower end of the body cavity of each polyp communicates, by a tubular process, with a common channel extending through the entire stem, a circulation of fluid, often containing granular particles, taking place through the whole colony. In the compound Actinozoa, the digestive cavities of the individual animals also

open into a chamber in the common fleshy basis, the aperture being radiate in shape, and capable of being closed by muscular contraction.

Protozoa.—Of these, the higher Infusoria alone possess any representative of an alimentary canal. In the paramecium, for example, a depression exists on the surface of the body, bordered by cilia, and leading to an aperture called the mouth, from which a short blind tube, named the gullet, dips into the sarcodous body. This is the last imperfect trace of a digestive canal, seen in the Animal Kingdom. Temporary cavities, formed by movements in the sarcode, into which food, or colouring matters may penetrate, appear like stomachs, whence the name *polygastric* applied to some of those microscopic creatures; but as these cavities may be seen slowly to move within the sarcode, up one side, and down the other, they are no longer regarded as stomachs. The undigested food, after thus circulating through the sarcode, is expelled at a particular point, either near the mouth, or near the hinder end of the body, which point is only then recognisable.

In the Sponges, Rhizopods, and Gregarinida, no trace of an alimentary canal exists. The system of canals with incurrent and excurrent apertures, seen in the Spongida, is not digestive more than it is respiratory or reproductive, but depends on the plan of construction of Sponges, which are composed of an open framework, supporting aggregations of astomatous amœbiform masses of sarcode, each of which directly assimilates food. In the solitary amœba, and its allies, the proteiform contractile sarcode applies itself to nutrient substances, and completely encloses them; digestion and assimilation take place within it, and the undigested portions are extruded at some indifferent point. The Rhizopods are nourished in a similar manner. The microscopic parasitic Gregarinida, appear like the *tœnia* and *echinocœci*, to imbibe nutrient matter directly by their surface, from the fluids of the intestine, perivisceral cavity, or other chambers or tissues of the animal, in which they live.

The Abdominal Digestive Glands.

Gastric Glands.—Gastric tubuli exist in the secreting portion of the stomachs of all the Vertebrata, becoming short and simple in the frogs and fishes. In the higher Mollusca and Annulosa, as in the Cephalopods, Pteropods, and perfect Insects, the stomach also has numerous follicles, probably analogous to gastric tubuli; but in the lower Mollusca and Annulosa, and in the Molluscoida and Annuloida, the walls of the gastric cavities are often destitute of distinct glands. This is the case also with the walls of the digestive canal in the Cœlenterata.

Liver.—This important organ, or some representative of it, is more widely distributed amongst animals than any other secreting or excreting gland. It is present as a well-defined organ, not only in all the Vertebrata, the amphioxus only excepted, but also in all the Mollusca and Molluscoida, and is represented in the Annulosa by tubular cœca or follicles, which are found even in the Annelida, and likewise in the Rotifera and Echinodermata amongst the Annuloida. No corresponding part, however, exists in those Annuloida which are destitute of a distinct alimentary canal, such as the Trematoda, Tæniada, and Acanthocephala, nor yet in the Cœlenterata, much less in the Protozoa.

Amongst the Vertebrata, the liver, proportionally to the body, becomes progressively larger in passing from the Mammal to the Fish. Its general form corresponds with that of the abdominal cavity; thus, it is broad in the apes and the Carnivora, longer in the larger Ruminant and long-bodied animals; of moderate length in Birds; broader in the comparatively short Chelonia and Sauria, but long in the elongated Ophidia; broad and short in the frogs and toads, but long in the newts; stretching widely into the abdomen of the broad-shaped skates and rays, but lengthened out in the eel. Its position is usually symmetrical, but in the Mammalia with large compound stomachs, it is placed more towards the right side, as is also the case in the anthropoid apes; in Fishes, generally, it lies more on the left side of the body. In Birds, in which the diaphragm is complete, the liver is notched for the reception of the heart and pericardium; in Reptiles, Amphibia, and Fishes, which have no diaphragm, the liver also reaches up to the pericardium, except when the body is very long, as in the serpents and eels.

The liver in the Mammalia generally, is nearly simple, its lobes being only slightly marked. In the Ruminants, it is subdivided into three lobes; in the Rodentia and Carnivora, there are from three to five lobes, viz. a central one, and one or two on each side; sometimes, it is further subdivided into small and irregular secondary lobules. In the llama, amongst Ruminants, the under surface, and in the capromys, a Rodent animal, the whole surface, is divided by deep fissures into angular masses, resembling those of the kidneys of the bear. In Birds, the lobes are two, and symmetrical; in Reptiles and Amphibia, the lobes are also generally two, but the liver is undivided in the Ophidia; in Fishes, the liver is often more subdivided. The microscopic structure of this gland, in all the Vertebrata, resembles that of the human liver. In the curious amphioxus, a long cæcal appendage from the intestinal canal, having a layer of greenish cells lining its interior, is regarded as a rudimentary liver, no distinct organ otherwise existing.

In the *Mollusca*, the liver is a large, symmetrical, solid, and lobulated organ, having two ducts. Its great development in these animals, and also, it may be added, in the cold-blooded Vertebrata, may be connected with the function of storing up fatty matter, as the adipose tissue does in the higher Mammalia. The nucleated hepatic cells in the Non-vertebrate animals, and also in the cold-blooded Vertebrata, contain much more simple oleaginous matter than they do in the warm-blooded Vertebrata, in which latter, the proper biliary fatty acids chiefly occupy the cells; in Birds, the cells contain less ordinary fat than in Mammals. Sometimes, as in the Cephalopods and Lamellibranchiata, the liver is subdivided into minute lobules, composed of branching ducts, ending in dilatations. In the Gasteropods, the ramified ducts and terminal follicles are more distinct, so as to form a loose compound racemose gland. The chief ducts are ciliated internally.

Amongst the Molluscoida, the Brachiopoda have a large, minutely lobulated liver, composed of ramified tubuli. As some of the earliest fossils yet discovered belong to this Class, a hepatic organ yielding bile, and, therefore, digestive processes corresponding with those known to us in the present day, must have existed in most remote periods of the earth's history. In the Ascidioida, the liver presents interesting gradations; for, in different cases, it may consist of a small

gland, a cluster of follicles, a single follicle, or simple lacunæ or laminae on the inner side of the intestine; it is represented only by a yellowish, orange-coloured, or brownish glandular spot, on the *hepatic portion* of the walls of the intestine. In the Polyzoa, the sides of the intestine below the stomach, are marked with brown hepatic tubes, follicles, or spots.

Amongst the *Annulosa*, the Crustacean liver is of a yellowish colour, large, and complex. In some kinds, as in squilla, it is symmetrical, lobulated, and sublobulated, each sublobule consisting of clusters of round follicles connected with a central duct. In the crabs and lobsters, the follicles of the liver are innumerable, much branched, and separated from each other. In the river crab, the follicles are less ramified. In the lowest Crustaceans, such as the parasitic argulus, the hepatic follicles are still more simple, or this organ consists only of a mass of nucleated cells.

In the highest Insects, and in the Myriapods, the liver is represented by hepatic tubuli, connected with the intestine; these are short and numerous in dytiscus, only two, but elongated, in blaps, or even single, as in the grasshoppers; sometimes they are mere vesicles. In no case is the liver massive, but always tubular. In the Spiders, the hepatic follicles are either short and simple, or they end in compact clusters of vesicles. In the Annelids, the liver is represented by gland cells, situated either in ramified tubes, as in Arenicola, or in tubuli ending in an oval sac, as in Aphrodita, or in numerous follicles, as in the leech.

Amongst the Annuloida, a single long follicle in the Trematode worms, represents the simplest form of rudimentary liver; in the parasitic Tæniada and Echinococci, the liver, as indeed the intestine itself, is unrepresented. In certain Echinodermata, as in asterias, coloured cells are found in the walls of the radiating prolongations of the gastric cavity, which perhaps secrete biliary matter.

In the Cœlenterata, no separate hepatic organ exists in connection with the simple digestive cavity; but the walls of this, as in veella, sometimes present a mass of gland cells, which may form bile. No such product has yet been found in any part of the unicellular Protozoa.

Blood-Vessels of the Liver.—In all the Vertebrata, the liver receives blood both from the hepatic artery and the portal vein. In the Mammalia, this vein, as in Man, has only a few communications with the lumbar and pelvic systemic veins. In Birds and Reptiles, the connection between the pelvic and portal veins is such, that a part of the blood from the lower extremities, and from the tail, joins the portal blood, and passes into the liver. In Fishes, the caudal veins, and sometimes those from the reproductive organs and the air-bladder, are connected with the portal system. In the Mollusca, the liver is supplied solely with arterial blood; the same is the case also in the Annulosa and Crustacea, indeed, in all Non-vertebrated animals which have blood-vessels.

Gall-Bladder.—In Mammalia, a gall-bladder is sometimes present, and sometimes absent. Amongst the herbivorous kinds, it is present in nearly all Ruminants, as in oxen, sheep, goats, and antelopes, but not in the camels and stags. It is also absent in Solipeds and in most Pachydermata, as in the horse, tapir, peccary, and elephant, but not in the pig. In the elephant, the hepatic duct is dilated and thickened, and has a spiral fold within. The gall-bladder is wanting in the mice and hamsters, amongst Rodentia; also in the sloths, amongst the Edentata, and

in the true Cetacea. In the carnivorous and insectivorous kinds, the gall-bladder is present. In the cat and a few other animals, it is sometimes double. When the gall-bladder is present, a cystic, hepatic, and common bile-duct exist.

In Birds, the gall-bladder is generally present, but is wanting in certain species of a particular genus, without obvious relation to its habits or food; it is absent in the ostrich, pigeons, toucans, and many parrots. Proceeding from the liver, in Birds, are two ducts, one hepatic, to the duodenum, the other to the gall-bladder, from which a cystic duct runs on to the duodenum; there is, therefore, no common bile-duct. When the gall-bladder is wanting, the two hepatic ducts open separately into the intestine.

In Reptiles, a gall-bladder always exists, but it varies in form. It is placed at a distance from the liver and has a long cystic duct, in the Ophidians; but it is imbedded in the substance of that gland in the Chelonians. There either is a common bile-duct, or the cystic and hepatic ducts open separately into the duodenum.

The gall-bladder invariably exists in Amphibia.

In Fishes, this receptacle is usually present, though it is absent in many genera, being then replaced by a dilatation upon one of the hepatic ducts, which are here usually numerous.

In the Mollusca and Molluscoida, in which the liver is massive, no gall-bladder is found; nor could such a receptacle exist in connection with the hepatic tubuli of the Annulosa and Annuloida.

Pancreas.—This gland, or some representative of it, is present only in the Vertebrata, and in the higher Mollusca. It is not so widely distributed amongst animals as the liver; and, moreover, it much sooner assumes a rudimentary form, in the descending series, viz. in the Fishes.

In Mammalia, Birds, and Reptiles, the pancreas occupies the concavity of the constantly present curvature of the duodenum. In Mammalia, when the duodenal mesentery is short or absent, as in the Quadrumana, Carnivora, Ruminants, and Solipeds, the pancreas is compact and elongated, with a portion extending towards the spleen, so that it may seem bilobed, as in Carnivora and Ruminantia, or even trilobed, as in the horse, the splenic portion being double; when, however, the duodenum has a wide mesentery, as in Rodentia, the pancreas forms an arborescent mass between the two layers of the mesentery, as seen in the rabbit and rat.

The typical number of pancreatic ducts, in the Mammalia, appears to be two, as indeed is the case in the early condition in Man, the upper and larger duct alone persisting. In the horse and dog, there are also two ducts, the lower one being the larger; in the dog, this latter opens separately into the duodenum, but the upper one enters it close to the bile-duct. In the lion, two ducts join the bile-duct, and enter the duodenum by a common orifice. In the rabbit, the upper duct is very minute, and the chief duct opens from 9 to 12 inches below the pylorus. In all cases, however, the pancreatic fluid is discharged into the duodenum. In certain Carnivora, as in the seal, and sometimes in the cat, the chief duct dilates into a reservoir, previously to entering the intestine.

In Birds, the pancreas is proportionally larger than in other Vertebrata, in part, perhaps, owing to the deficiencies in the salivary glands. It usually consists of from two to six elongated portions, attached, as

usual, to the much bent duodenum. Each portion of the gland has a duct, generally opening separately into the intestine. There are six ducts in the vulture, fowl, heron, and grebe, three in the crow, pigeon, grouse, and duck, but only one in the eagle, quail, ostrich, and stork. In the stork alone, the single pancreatic duct opens, by a common orifice, with a single hepatic duct. Usually, one at least of the pancreatic ducts, in Birds, opens above the bile-duct, but this is not constant; when several pancreatic ducts exist, they usually open alternately with other hepatic or cystic ducts; the cystic duct generally opens lowest. The bile and pancreatic juice must be speedily, and almost simultaneously, mixed with the food. In the ostrich, however, these secretions are mixed with the food at some distance apart, the bile escaping through the single hepatic duct, close to the pylorus, and the pancreatic juice also by a single duct, 3 feet lower down.

In Reptiles, the pancreas is usually large. It is larger in the herbivorous than in the carnivorous Saurians, being largest in the iguanas. In the Chelonians, this gland is even ramified, as it is in the Rodents. In the Ophidians, it is either long and bifid, pyramidal, or round. The duct is nearly always single, and generally enters the duodenum separately, but sometimes with the bile-duct. In the Serpents, the pancreas is joined to the spleen, and has even been confounded with it.

In the Amphibia, the pancreas is found in the mesentery, between the stomach and duodenum; it is smallest in the purely aquatic species, such as the tritons. In the frog, the bile-duct perforates the pancreas, and, it is believed, receives small pancreatic ducts in its course. In the lowest Amphibia, as in the siren, the pancreas is much subdivided, so as to approximate to the form of the pyloric appendages in the Fishes; its ducts are no longer united into one, or into a few principal trunks, but form numerous parallel canals, opening separately into the duodenum.

In many Fishes, there are found, opening into the duodenum, near the pylorus, certain simple tubular or ramified follicular prolongations of the coats of the intestine, lined by a glandular membrane, named the *pyloric appendages*. The food does not enter them, and, from their position and glandular character, they have usually been regarded as the homologues of the pancreas, but they are somewhat anomalous organs. In the sturgeon, these appendages are so numerous as not to have been counted; the cod and whiting have about 120, the salmon 60, averaging $6\frac{1}{2}$ inches in length, the sprat 9, the perch 3, the turbot 2, and the ammodytes and polypterus only 1. They are entirely absent in many Orders. When few in number, they open separately into the intestine; but when numerous, they combine into clusters, each opening by a single orifice. Thus, 50 cæca, in the pilchard, open by 30, and in the tunny by only 5 orifices; in the swordfish, there are only two openings, and, in the sturgeon, the multitudinous cæca open by a single short duct. They are largest and most numerous in fishes of active digestion and rapid growth, and, on the whole, most developed in the more voracious tribes. They are more commonly few and large in the Osseous fishes, whilst in the Cartilaginous group they are usually smaller and numerous. When absent, the mucous membrane of the intestine below the pylorus, is, sometimes, as in the eel, thick, vascular, and glandular, and yields, on pressure, a copious secretion.

The pyloric appendages are certainly glandular organs and not in-

testinal diverticula, intended for purposes of absorption; but it has been suggested that they are special glands, and that the true representative of the pancreas in Fishes, is a small gland sometimes found attached to the liver. Such an organ exists in the carp, pike, silurus, sturgeon, and ray, in which fish it is large and has a duct opening near the bile-ducts, and in many other species. In some instances, it would seem to be a detached portion of the liver, but in other cases, its pancreatic structure is undeniable. Certain fish, as, for example, the trout, possess this organ as well as the pyloric appendages; in others, it is very small; in some, it is not found, but may then be represented by glandular structures in the walls of the intestine. Bernard, who doubts the pancreatic character of the pyloric appendages, asserting that their secretion is acid and viscid, like the intestinal juice, and not alkaline and diffuent, like the pancreatic juice, states that a watery emulsion of the *proper* pancreas of the ray, converts starch into sugar, and decomposes fatty matters into their proper fatty acids and glycerin, like the secretion or substance of the pancreas of the higher Vertebrata.

In certain Cephalopods, a laminated and folliculated sac, connected with the two hepatic ducts, in other Cephalopods, a spiral appendage, and, in many Branchio-gasteropods, as in *aplysia* and *doris*, a long cæcal glandular tube, which communicates with the intestinal canal below the stomach, may represent a molluscan pancreas.

In the Annulosa, the Insects and some others, have tubuli, connected with the upper part of the intestines, which may be pancreatic. Similar rudimentary parts exist in the Rotifera, amongst the Annuloida. In cases in which such tubuli are not present, gland cells are sometimes found in patches upon the lining membrane of the intestine. Sometimes even these are not distinguishable.

Intestinal Glands.—In all the Vertebrata, besides structures resembling the closed sacs of the solitary and agminated glands, the intestinal tubuli or crypts of Lieberkühn exist. In Mammalia and Birds, and probably in Reptiles, Amphibia, and the higher Fishes, racemose mucous glands are found in the duodenum.

The tubular or saccular appendages, the short cæca, or the minute patches of glandular epithelial cells, distinguished by their colour and contents, which are found in the Molluscos, Annulose, and lower allied forms, are probably not representatives of the intestinal tubuli in the higher animals, but rather of the liver and pancreas. Indeed, the intestinal canal is itself so minute in many of these lower animals, that its lining membrane is almost of necessity simple, smooth, and covered throughout with a delicate epithelium only.

The Chemical Processes of Digestion in Animals.

In studying the action of the digestive fluids, physiologists have employed not only the human secretions, but also, and sometimes exclusively, those collected from fistulæ in animals, and likewise artificial fluids made by macerating the glands in water. The properties of these several secretions having been established experimentally, in regard to *certain* vertebrate animals, it is reasonable to conclude that, wherever these particular glands exist, the respective secretions possess similar, if not identical, properties.

The *saliva* is most abundant in herbivorous and granivorous animals, in which the quantity of food to be moistened is greater, and the special action of this fluid on starchy matter is most required; in carnivorous and insectivorous creatures, this action is not necessary, and the secretion is less plentiful, being used rather for purposes of lubrication; or, as in Fishes, it may even be wanting. Nevertheless, the saliva of the dog, taken from the mouth, converts starch into sugar, though somewhat slowly. It is said, however, that the secretions of the parotid and submaxillary glands in the dog, and even of the parotid only, in the horse, are by themselves, and unmixed with the mucus of the mouth, incapable of effecting this transformation.

In those Mollusca, Annulosa, and Annuloida, in which, as in Cephalopoda, Insecta, Myriapoda, and Rotifera, glands, called salivary, exist, the exact properties of the secretion, and its chemical action on the food, have not yet been determined; but it is usual to regard those glands, whether tubular or follicular, which open into the upper part of the alimentary canal, as salivary glands. On similar grounds, gland structures opening into the stomach are considered as gastric glands; those connected with the upper part of the intestine, as hepatic, or hepatic and pancreatic; and, lastly, those emptying themselves into the lower part of the intestine, as excretory, and probably renal.

As albuminoid substances are essential to the formation of all animal tissues, the *gastric juice*, which acts upon them, would appear to be likewise an essential solvent in the digestive function of every animal. Hence, it is probably present in all animals, certainly in the lowest which possess a stomach, and even in the Coelenterata. When no distinct gastric tubuli exist, the peptic agent is secreted by the cells of the lining membrane of the digestive cavity.

The stomachs of Fishes, after death, are often rapidly digested by their own gastric juice; whereas this occurrence is much less frequent in Man and Mammalia. This has been referred to the small difference of temperature which takes place after death, in a fish, as compared with a warm-blooded animal. The gastric juice of fishes habitually acts at a low temperature; whilst that of the warm-blooded animal operates at a much higher temperature. It is said that the gastric juice of fishes loses its peptic properties at the ordinary temperature of a warm-blooded animal, and inversely, that the gastric juice of the warm-blooded animal acts slowly, or not at all, at the temperature of the fish; and, moreover, that the solvent powers of the gastric juice of a Mammal are not lost, until it has been heated to 120° ; whilst in the case of the fish, they are lost at 80° (Brinton). If this be confirmed, it shows a remarkable modification of the properties of the same secretion, in different animals having particular conditions of existence. It would be interesting to note whether post-mortem digestion of the gastric cavity of the non-vertebrated animals ever takes place.

From its peculiar colour, the *bile* can be easily recognised. It may thus be detected in those Annulose and Annuloid animals, even in the minute Rotifera, in which the liver is not massive, as it is in the Vertebrata, Mollusca, and higher Molluscoida, being represented only by hepatic tubuli; coloured secretions are also detected in the gland cells of still lower animals. The office of the bile must be similar in all animals in which it is found.

The peculiar property of the *pancreatic juice*, that of emulsifying and decomposing fat, has been shown by Bernard, to exist not only in Mammalia, but also in Birds, Reptiles, Amphibia, and Fishes, as, for example, in the goose, turtle, frog, salamander, and ray. Moreover, he asserts that, when the pure saliva, in any animal, is incapable of converting starch into sugar, the pancreatic fluid possesses this property.

The action of the *intestinal juice* upon food, has been shown to be in the higher animals, as in Man, supplementary to that of the other secretions. In the lower animal forms, in which the intestinal tubuli come to represent important glands, an analogous blending of function may prevail.

The organic food of all animals, whether derived from other animals or from plants, consists of similar proximate chemical substances; and the solution of these is probably accomplished, in all cases, by processes of a similar nature. But our knowledge of the specific chemical differences, and modes of action, of the digestive fluids in different animals, is yet imperfect. In the Mammalia, and perhaps in all Vertebrata, the composition and action of the fluids resemble those observed in man. The gastric juice of the herbivorous sheep and calf dissolves animal food, as readily as that of the omnivorous pig and carnivorous dog. But many modifications, yet undiscriminated by the chemist, doubtless exist, as illustrated by the ascertained varieties in the acids of the gastric juice and the bile, in certain Mammalia and Birds (pp. 65, 77). Still more important differences in composition and power may exist, especially in the lower tribes, in some or all of the digestive secretions, adapting them to the solution of substances, ordinarily indigestible. Thus cellulose, lignin, and even resinoid bodies from the vegetable kingdom, and yellow elastic tissue, cartilage, and the horny, chitinous, and coriaceous integuments from the animal kingdom, are eaten and probably partially digested by certain insects and other creatures, though usually those substances resist digestion.

In the complex alimentary canal and glandular appendages of the Vertebrata, Mollusca, and Annulosa, in the more simple digestive system of a polyzoon, or of a rotiferous animalcule, and even in the digestive cavity of the hydra, with its single external opening, its communication with the cavity of the body, and its want of distinct glandular appendages, the digestive secretions are always produced by glandular epithelial cells, whence they are discharged into the alimentary canal, at suitable points, to act upon the food. In the absence of massive or tubular glands, or of clusters of special cells, it is even possible that adjacent cells, nearly or quite similar under the microscope, may perform the office of different glands. Digestion, in the hydra, may be as complex a process, regard being had to the chemical composition of its food, as in the highest Vertebrata. So long, indeed, as we recognise in any animal a distinct digestive cavity, we may reasonably infer the occurrence of a digestive process, rendering different nutrient substances soluble and absorbable. The starchy, albuminoid, fatty, and the less digestible substances used as food, must require their peculiar transmuting, liquefying, or emulsifying solvents, produced in infinitesimal quantity, but acting with characteristic power. It is observable, however, that of these fluids, the peptic and emulsifying agents are the most essential, specific, and universal: for in the cold-blooded aquatic animals, whether vertebrate or non-vertebrate, such as the voracious

Fishes, and the carnivorous Mollusca and Cœlenterata, there is little or no necessity for a salivary fluid capable of transmuting starch; whilst even in the lowest animals, fatty and albuminoid substances are essential constituents alike of the bodies and of the food. The low temperature of these animals, and the higher temperature of the starch-feeders generally, are interesting facts, in connection with the heat-producing power of amylaceous diet.

In the unicellular Protozoa, whether, as in the Infusoria, there exist a short tube leading into their interior, or, as in the Sponges and Rhizopods, no digestive cavity at all, solid food must also be dissolved by some action of the animal, before it is absorbed; though these universally aquatic creatures may be partly nourished by materials already dissolved in the surrounding medium.

In the case of the parasitic Gregarinida, and even of certain of the annuloid Entozoa found in the alimentary canal of other animals, the nutrient substances absorbed are probably those which have already been digested, and so prepared for absorption by the gastric and other secretions of those animals, a sort of vicarious digestion being here employed. In those Entozoa, however, which infest other organs or tissues, such as the air-tubes, muscles, brain, and interior of the eyeball or blood-vessels, probably, little or no digestive change of the nutrient materials is required; the nutritive function consists merely of imbibition and assimilation, observed in the ultimate nutritive processes in the higher animals, and digestion is merged in nutritive absorption.

ABSORPTION.

By the process of digestion, the food is reduced to a compound alimentary basis, composed of aqueous, saline, extractive, mucilaginous, saccharine, amylaceous, oleaginous, and albuminous matters, sometimes mixed with alcoholic, ethereal, acid, pungent, odoriferous, and colouring substances. The materials of this complex pabulum, whilst retained within the digestive cavity, remain, strictly speaking, *external* to the living frame; but a process immediately ensues, by which they are, sooner or later, taken up into, and enter, the living tissues; this is termed *Absorption*. The chief object of this process of the *absorption of food*, is the introduction of new material, for the repair of the continuous waste of the living body.

Absorption, however, considered as a physiological function, consists of more than the mere taking up of nutrient materials from the interior of an alimentary canal, or of a simple digestive cavity, or at the surface of a unicellular animal organism. It includes that general process by which all external soluble substances, whether solid, fluid, or gaseous,

Fig. 100.

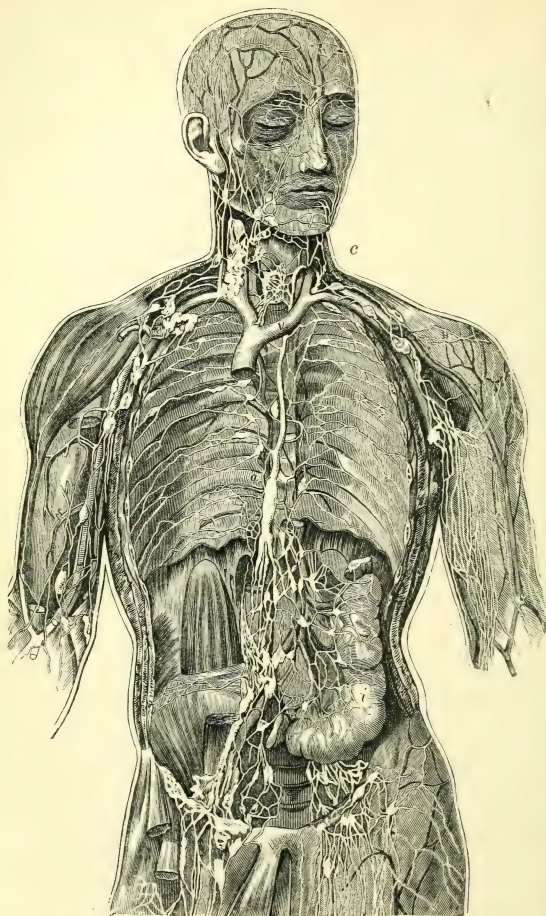


Fig. 100. General view of the principal absorbent or lymphatic vessels and glands. The superficial lymphatics are shown on the head and face, and on the left limbs; the deep lymphatics on the right limbs. The lym-

beneficial or poisonous, nutrient, stimulant, or respiratory, are introduced into the tissues of the body, through any natural or artificial surface whatever. Moreover, it comprehends, in part at least, another process, by means of which portions of the living tissues are themselves removed, or absorbed, within the body. The former of these two processes is sometimes named *general absorption*, and the latter, *intrinsic* or *interstitial* absorption. Intrinsic absorption is essentially a nutritive process. The term extrinsic may be applied both to general absorption and to the absorption of food.

The Absorbent Vessels and Glands.

In Man, and the Vertebrata generally, two sets of vessels are engaged in the processes of absorption, viz. first, certain *blood-vessels*, especially the *venous capillaries*, and the *smaller veins*; and, secondly, the *absorbent* vessels proper.

The absorbents of the body generally, which always convey the transparent *lymph*, and are named the *lymphatics*, commence, by networks, near the various membranous surfaces, and in the interior of certain tissues and organs. Their number, in any part, seems to be proportionate to the quantity of areolar tissue which it contains, rather than to the number of its bloodvessels, or the activity of its functions; thus, lymphatics have not been found in the brain and spinal cord, and only a few in the muscles; but in the subcutaneous areolar tissue, and in the intercellular spaces, they are very abundant. They are numerous in the serous and synovial membranes, but still more so on the mucous membranes and skin. The trunks from the commencing lymphatic networks (fig. 100), either proceed in company with the bloodvessels, thus forming the *deep lymphatics*, or else run on the *surface* of organs, or in the subcutaneous cellular tissue of the body and limbs, so forming the *superficial lymphatics*. From all parts of the body, they

phatic glands are seen in the neck and axillæ, at the elbow, in the groins, pelvis, and abdomen; a part of the small intestine, *i*, shows its chief lymphatic or lacteal trunks, passing on to the mesentery, through the mesenteric glands, to the upper and back part of the abdomen. *a*, the chief trunk of the absorbent system, named the thoracic duct, commencing below, in a dilatation, named the *receptaculum chyli*, and curving down in the neck at *c*, to end in the great veins at the root of the neck, where the jugular and subclavian veins join to form the left innominate vein, *v*. On the right side of the neck, smaller lymphatic trunks are seen entering the great veins.

run towards the root of the neck, where they end in the venous system. More numerous than the bloodvessels, they pursue an irregular course, often unite and again divide, and present, in certain situations, as especially seen in young subjects, small *retia mirabilia* or *lymphatic networks*, enclosed in a thin areolar investment. They, moreover, pass through the bodies known as *lymphatic glands*, which may be regarded as more highly and specially developed retia (p. 66). Ultimately, the lymphatics of the lower limbs, of the lower half of the trunk, of the left side of the head and neck, and of the left upper limb, join the great trunk of the lymphatic system, the *thoracic duct*, *a*. Those from the right side of the head and neck, and right

Fig. 101.

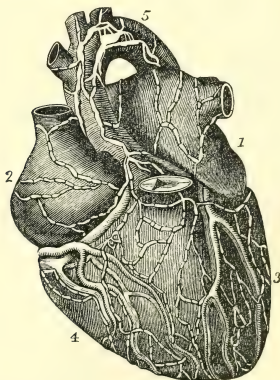


Fig. 101. Superficial lymphatics upon the heart, situated beneath the serous coat or visceral part of the pericardium. The figure also serves to show the shape, position, and subdivisions of the heart. 1, the left, 2, the right auricle; 3, the left, 4, the right ventricle; 5, the descending part of the arch of the aorta.

upper limb, unite to form a small separate trunk, named the *right lymphatic duct*. This enters the venous system at the point of junction of the right jugular and subclavian veins, its orifice being guarded by a double valve. A few separate and smaller lymphatic trunks are also said to enter the veins of the neck at different points. All the organs of the thoracic and abdominal cavities, have superficial as well as deep lymphatics belonging to them, figs. 100, 101. The lymphatics

were first described by Fallopius (1561), but afterwards much more fully, by Rudbeck and Bartholin; the thoracic duct was detected by Eustachius (obit. 1570).

The thoracic duct (fig. 100 *a*), begins below by a dilatation, named the *receptaculum chyli*, usually placed upon the second lumbar vertebra. From this point, the duct ascends, somewhat tortuously, in front of the vertebral column, into, and through, the thorax. Placed, at first, a little to the right of the aorta, it passes, opposite the third dorsal vertebra, behind the arch of that vessel, crosses over the œsophagus, and ascends on its left side to the root of the neck, *c*, where it curves downwards and outwards, behind the great bloodvessels, and finally opens into the angle of junction of the left internal jugular and subclavian veins, the entrance being guarded by a strong double valve. The thoracic duct measures from eighteen to twenty inches in length, and from two to three lines in width; it is somewhat varicose, or constricted at intervals, owing to the presence within it of numerous double semi-lunar valves, which have their free margins directed upwards, so that they are closed by downward pressure, and support the weight of the column of fluid contained in the duct. At the root of the neck, the contents of the absorbent system are poured into the venous system, and are mixed with the venous blood flowing towards the heart, regurgitation from the veins to the absorbent trunks being prevented by the valves placed at the opening of the latter into the veins.

The coats of the lymphatics, as elsewhere explained, are remarkably thin, and therefore highly permeable to fluids. The trunks themselves are very difficult to find, and even the thoracic duct eludes an ordinary dissection.

Lymphatic *glands* are found (fig. 100) in the arm-pits and groins, and a few at the bend of the elbow, and in the ham, where they are named respectively *axillary*, *inguinal*, *anti-brachial*, and *popliteal* glands; chains of glands, on each side of the neck, are named the *cervical* or *concatenated* glands; in the thorax, numerous glands, placed around the great air-tubes or bronchi, and usually containing a black deposit, are named *bronchial* glands; lastly, in the pelvis and abdomen, are the *iliac*, *lumbar*, and *mesenteric* glands.

Like general absorption, the absorption of food from the alimentary canal, is performed by the agency not only of the *bloodvessels* but also of the *absorbents* proper; those of the small intestines, which occasionally—that is, during digestion—

convey the milky white fluid, *chyle*, are named the *lacteals*, or *chyliferous* vessels.

The *arteries* of the intestine, chiefly derived from the mesenteric arteries, subdivide and inosculate in the mesentery, forming numerous vascular arches before they reach the attached border of the intestine; entering and ramifying in the submucous coat, their branches penetrate, and further subdivide in, the mucous membrane, in which they end in close networks of *capillaries*, near the mucous surface, around the intestinal tubuli and glands, and within the countless villi. From the capillary networks, the minutest *venules* proceed, and soon join to form larger veins, running to the attached border of the intestine; beyond this, the veins unite in the mesentery into still larger trunks; these, with the veins of the stomach, pancreas, and spleen, ultimately form the portal vein, which enters, and subdivides in, the liver. The veins from the lower part of the large intestine, however, do not enter this portal system, but join the veins from the lower half of the body; so, too, the veins proceeding from the mouth, pharynx, and gullet, enter the general venous system.

The *lacteals*, which may be said to be limited to the small intestine, below the entrance of the bile-duct and pancreatic duct, resemble the lymphatics of the stomach, large intestine, and other parts of the body, and, like them, convey, when not engaged in absorbing food, only a transparent lymph. The lacteals were discovered by Aselli (1622); their connection with the thoracic duct was shown by Pecquet (1651). In the mucous membrane of the stomach and large intestine, the absorbents probably arise by networks, like those of other membranes. In the small intestine, however, which is the proper seat of lacteal absorption, besides a network near the general mucous surface, absorbent vessels, which form, as it were, the *radicles* or absorbent extremities of the lacteal system, commence within the villi which specially characterise this part of the intestinal canal. These villi, during digestion, project into the pulpy digested food, as the rootlets of a plant, with their absorbing spongioles, depend in water or penetrate the soil.

The lacteals commence within the villi by closed extremities, and not by open mouths (fig. 102, 1). By some anatomists they are said to arise by a plexiform network, which, at the base of the villus, passes into larger vessels. According to others, a single lacteal vessel occupies the centre

of each villus, commencing near the apex by a simple closed extremity, by a dilated ampulla, or by a loop, which may be part of a network, and ending in the general network at its base. The diameter of the lacteals in the villi, is from $\frac{1}{1000}$ to $\frac{1}{800}$ of an inch. The network at their base, consists of a finer and a coarser layer, in the latter of which the vessels possess

Fig. 102.

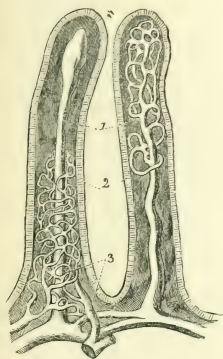


Fig. 103.

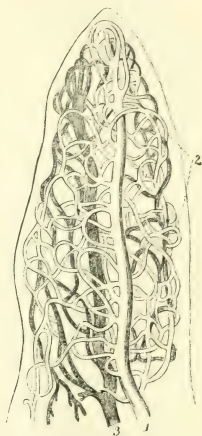


Fig. 102. Two intestinal villi highly magnified, showing the two supposed modes of commencement of the lacteals, 1, in their interior; one mode, by a dilated ampulla, the other by a network. The columnar epithelial cells, 2, covering the villi, are also shown; and likewise a portion of the capillary network, 3, lying outside the lacteal vessel. The larger lacteals at the base of the villi are indicated.

Fig. 103. The artery, capillary network, and vein of an intestinal villus artificially injected. The light-coloured vessel represents the minute artery which conveys the blood into the villus; the dark vessel is the vein along which the blood returns; the intermediate capillary network is marked 2.

valves. (Teichmann.) The villi are also very vascular, each containing a minute arterial and venous twig, with a close capillary network outside the lacteal vessels (fig. 102, 3, and fig. 103). The substance of the villus consists of a delicate extension of the mucous membrane, composed of a mixed, soft, areolar and granular tissue, containing fatty particles; further,

each villus contains, around the central lacteal, a few unstriped muscular fibres, by the contraction of which the villus may be shortened, and its substance thrown into transverse folds; lastly, the epithelial covering of the villus, which measures only about $\frac{1}{1200}$ of an inch in thickness, is composed, like that of the intestine generally, of a single layer of columnar nucleated cells, pointed at their attached end, but wider, flattened, and more or less polygonal at their free extremity. This part of the cell has been described as being ciliated, but the appearance is generally attributed to the existence of fine lines passing from the free end to the interior of each cell, and regarded by some as pores. In animals killed while lacteal absorption is going on, these epithelial cells are frequently found to be distended with fatty matter, the villi having a swollen and tuberculated aspect. At this time also, the central lacteals of each villus, and also the subjacent vessels, are found distended with whitish or bluish chyle. Upon the surface of the small intestine (fig. 104, 1), running beneath the peritoneal coat towards its attached border, are seen larger chyloferous vessels, proceeding between the layers of the mesentery, 2, 2; thence others, passing through the *mesenteric* glands, 3, converge to the back of the abdomen, where they end in the *receptaculum chyli*, or dilated part of the thoracic duct (fig. 100, a). If this duct be tied immediately after death, in an animal killed during digestion, it, as well as the chyloferous vessels generally, becomes much distended, and either of these vessels may burst, and the chyle may be extravasated at many points.

Beneath the mucous membrane in various parts of the alimentary canal, as in certain recesses at the root of the tongue (p. 54), and in the tonsils (p. 27), or scattered singly over the internal surface of the stomach, small intestine, and large intestine, and, lastly, collected in patches in the small intestine, there exist peculiar saccular bodies, called glands, which, however, do not appear to belong to the secreting gland system, but perhaps rather to the absorbent system. They are neither racemose glands, like the glands of Brunner, nor open follicles, nor tubuli, like the gastric glands and the crypts of Lieberkühn, but *closed sacs*, not communicating with the interior of the intestine, unless under some exceptional conditions. In the stomach and intestine, these bodies exist in two forms. First, as the so-called *solitary* glands of the stomach (p. 61), small intestine (p. 82), and large intestine

(p. 82), scattered over the mucous surface, as small soft whitish bodies, somewhat prominent, and about one line in diameter, or the size of a millet-seed when they are fully distended. Each sac consists of a thickish soft capsule, composed of an indistinctly formed areolar tissue, mixed with nuclei, and encloses a semi-opaque, adherent, and semi-fluid granular matter, containing mixed fatty and albuminous molecules,

Fig. 104.

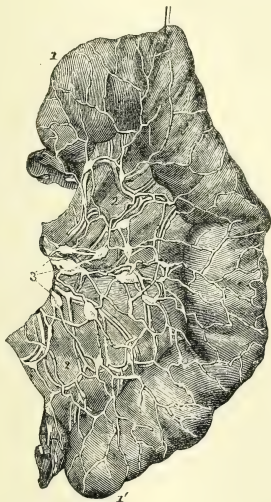


Fig. 104. Portion of the small intestine, 1, 1, with its mesentery; 2, 2, showing the superficial lacteal vessels in the intestine and mesentery. The mesenteric glands are also seen at 3, and elsewhere.

nuclei, and cells, amongst which loops of capillary vessels are said to penetrate from all sides. The mucous membrane passes completely over these sacs, and usually even a few villi are placed upon them. In the large intestine, they are situated at the bottom of a wide recess, having a narrow orifice, which has been erroneously regarded as an opening into the sac. Secondly, clusters of these sacs, the *agminated glands*, or Peyer's glands (Peyer, 1677), are found in the small intestine only. These Peyer's patches, twenty to thirty in number, are either rounded

or oval, being from half an inch to three or more inches in length, and about half an inch or more in width; they are placed at intervals, longitudinally along the free border of the intestine (Fig. 91). Commencing, of small size, in the lower part of the duodenum, they gradually become more frequent and larger in the jejunum and upper part of the ileum, but are largest and most numerous in the lower part of the ileum. Their component sacs (Figs. 98, 99) exactly resemble in structure the single sacs of the so-called solitary glands. When distended, as occurs during the absorption of food, the patches of Peyer's glands present a whitish speckled appearance, and, if moderately magnified, each sac is seen to be surrounded by a little zone of darkish points, which are the mouths of the crypts of Lieberkühn, thrust outwards by the filling of the sac. The mucous membrane over the sacs, is entire. Villi are seen in the intervals between them and sometimes, as is the case with the solitary glands, even upon them. Opposite these patches, the submucous coat of the intestine is more vascular than elsewhere, and especially abounds in lymphatics, which, however, have not been traced into the sacs, but here form plexuses of large and easily injected vessels.

The sacs of both the solitary and the agminated glands are sometimes found open, as if by rupture through distension; but from their normally closed condition, the fatty and albuminoid nature of their contents, the abundance of lymphatics in their neighbourhood, and from the special distension of these, as well as of the sacs themselves, during the process of intestinal absorption, it is with much reason inferred, that both the solitary and agminated glands are concerned, in some way, in this last-named function; the mode in which they act, and the precise nature of their office, are, however, not yet understood.

Endosmosis, Exosmosis, Osmosis, Liquid Diffusion, and Dialysis.

The absorption of liquids, or of substances in a state of solution, by the living animal body, is either a simple filtrating process, connected with the fine *porosity* of the tissues; or it partakes of the character of *dialysis*, or the penetration of liquid or dissolved substances through a moist membrane permeable to such bodies, without being directly porous, like a filter; or, lastly, it may be connected with special *selective* or *repellent* actions in the living tissues. Even in the last case, the process may be physical, i.e., either filtrating or dialytic. The penetration of dissolved substances through the tissues, occurs, not only in

general absorption and the absorption of food, but also in intrinsic absorption, in all acts of nutrition, in the reabsorption of the disintegrated materials of the body itself, likewise in the various acts of secretion and excretion, in certain processes of the function of respiration, and of those of taste and smell.

Endosmosis.—The action of the living tissues, in these several functions, has, since the researches of Dutrochet (1827), been in part referred to the physical processes of so-called *endosmosis* and *exosmosis*, or the passage of fluids in opposite directions through dead animal membranes (*ἔνδον*, *endon*, within; *ὄσμος*, *osmos*, impulse). It was first pointed out by Parrot, of St. Petersburg (1803), that, if two liquids of unequal density are separated by a permeable organic membrane, a mutual but unequal interchange takes place between them; but Dutrochet more fully investigated the subject. His *endosmometer* consists of a bell-shaped glass, covered at its mouth with a thin animal membrane, and fitted at its upper end with a graduated tube; a coloured solution of sugar, gum, or some saline substance, being introduced into the glass, the covered mouth is then immersed in water, when it is found that the solution rises in the graduated tube, to a considerable height above the level of the water around it. This phenomenon Dutrochet named *endosmose*. During its occurrence, however, some of the dissolved substance contained in the tube, passes into the water outside, and this process he named *exosmose*. The more rapid flow, however, usually takes place from the rarer to the denser fluid; and hence, if the endosmometer be filled with water, and be dipped in the solution, the more active, or so-called endosmotic current, really passes *outwards* through the membrane. Dutrochet pointed out that the force of endosmosis bears a certain ratio to the density of the inner fluid, and that the quantity of fluid which passes, depends also on the extent of the membrane. To avoid the effects of gravity, he from time to time adjusted the endosmometer, so that the fluids inside and outside, were kept on a level. He showed that capillarity, or capillary ascension, does not account for the phenomena, which, he admitted, cannot be satisfactorily explained. He supposed that endosmosis and exosmosis are peculiar to organic membranes, and that they explain the rise of the sap in plants, many processes of the animal body, and probably also the motions of various vegetable and animal fibres and cells.

More recently, these physical phenomena have been studied by Bécclard, Matteucci, Graham, and others. The direction of the current through an animal membrane, is not always found to be from the lighter to the denser fluid; for water passes more rapidly into alcohol, than alcohol into water. The great endosmotic tendency of water has been attributed to its high specific heat, which is higher than that of any other fluid. (Bécclard.) But the properties and qualities of the various fluid, or saline and other soluble, substances, are also found to influence the result. The phenomena are favoured by moderately high temperatures, by pressure, by the saturation of the membrane with acids or alkalis, by special relations between the membrane and one of the fluids, and by the constant removal of the endosmosing fluid by motion or by evaporation.

Professor Graham has examined separately, first, the tendency of different liquids or solutions to mix with each other directly, and,

secondly, the influence of a permeable membrane interposed between them. The former phenomena constitute *liquid diffusion*, and the latter *osmosis*, or *dialysis*.

Liquid Diffusion.—A phial, with open mouth, is filled, nearly to the top, with a given solution, and is then placed in a larger vessel, into which water is carefully poured, so as to stand considerably above the level of the mouth of the phial; or a graduated jar is filled, up to the highest mark but one, with water, and then, by means of a pipette, the solution to be tried is poured in at the bottom of the jar, so as to elevate the water to the top of the scale. On leaving phials or jars, so prepared, standing, without agitation, or change of temperature, the substance in solution ascends in the water, against the influence of gravity, as if it were volatile. In other words, it diffuses; hence the term liquid diffusion. All soluble substances diffuse in this way, but they are not equally diffusible. Thus, in phial experiments, the relative quantities of the following substances, diffused through the water above, from solutions of like concentration, in the same time, are as follow: chloride of sodium 58, nitrate of soda 57, sulphate of soda 27, cane sugar 26, gum 13, and albumen 3. In jar experiments, the relative times of diffusion of equal quantities of different substances are these: hydrochloric acid, the most diffusible substance hitherto tried, 1; chloride of sodium 2·3; sugar 7; sulphate of magnesia 7; albumen 49; and caramel, or burnt sugar, 98. The rate of diffusion of different substances is, therefore, remarkably different, being very high for hydrochloric acid and chloride of sodium, but low for gum, albumen, and caramel. So distinct and constant is the diffusive power of different substances, that, from mixed solutions of these, chloride of potassium ascends more rapidly than common salt, and this, faster than sulphate of soda; with salt and albumen, the difference is still more marked. Weak chemical compounds may even be decomposed through the different diffusive power of their constituents; thus, alum, a double sulphate of alumina and potash, is decomposed, in a phial diffusion experiment, by some of the sulphate of potash rising away from its associated sulphate of alumina.

The rate of diffusion, in proportion to the quantity of the substance diffused, is greater when the solution is weak; but the absolute quantity diffused is greater with strong solutions. Heat increases the rate of diffusion, common salt, e. g. diffusing $2\frac{1}{2}$ times more rapidly at 120° than at 60° .

From various points of contrast, including their behaviour as diffusible bodies, chemical substances are arranged by Graham into *crystalloids* and *colloids*.

Crystalloid bodies are hard, rigid, and quickly soluble; their solutions are never viscous; they are always more or less sapid; their chemical reactions are quick and energetic, but in a molecular sense, they are, if left to themselves, static, or little liable to molecular changes. This class includes every crystallisable body, and every substance capable of entering into the formation of a crystalline body.

Colloid substances do not crystallise, but are amorphous; they have, when dry, a vitreous structure, and instead of being hard and brittle, are soft or tough; they dissolve freely but slowly, their solutions being more or less viscous, and they gelatinise on cooling, or

by concentration. Hence they are named colloids, from collin or gelatin, and sometimes pectoids, from their gummy character; they are tasteless or insipid, but they may give rise to sapid crystalloids; their combining equivalents are high, and their molecules accordingly heavy; as acids, or bases, they are chemically inert, but they are liable to remarkable molecular changes, and, in this sense, exhibit great dynamical activity; they have a weak affinity for water, and are easily thrown down from their solution in it. They readily undergo metastasis, passing from a state of solution into the gelatinous, pectous, or solid condition, and, with time, even into the crystalloid state, either spontaneously, or by the slightest contact with extremely minute portions of other substances; thus a solution of silicic acid is gelatinised by $\frac{1}{10000}$ part of an alkaline or earthy carbonate. Lastly, in their soft condition, they form, like water, media for liquid diffusion, a crystalloid body diffusing itself through a jelly, almost as readily as through water itself. Colloid substances include gelatinised starch, dextrin, gum, caramel, gelatin, albuminoid bodies, vegetable and animal bodies, extractives, and a number of soluble hydrated mineral substances, as, for example, silicic acid and peroxide of iron.

Of the two great classes of substances thus distinguished, crystalloids are highly diffusible, whilst colloids are of low diffusibility.

Finally, liquid diffusion is to be regarded, not as a purely physical process, like the diffusion of gases, which depends on a tendency of those elastic fluids to intermix in inverse proportions to their density; nor is it to be explained by capillarity; for the diffusion of different substances does not coincide with their ascension in capillary tubes; but this process appears rather to depend on chemical action. The high diffusibility of crystalloids is explained by their powerful attraction for their solvent, the mobility or volatility of which is determined by their presence; whilst the low diffusibility of colloids is referred to their feeble combination with their solvent, on the volatility of which they accordingly have little effect.

Dialysis.—The phenomena of the diffusion of liquids into each other are rendered more definite by the interposition of permeable membranes between them. If a gutta-percha hoop be closed on one side with vegetable parchment, the tray thus formed will not allow water to pass through it by filtration. By supporting, or suspending, such a tray in a large vessel of water, and pouring a thin layer of the fluid or solution to be experimented upon, into it, *dialysis*, or diffusion through the permeable membrane, takes place. Crystalloid bodies, in solution, pass through the membrane, or dialyse, into the water, with great rapidity; whilst colloid bodies are almost absolutely prevented from passing. Thus, in equal times, the proportion of common salt which dialyses is 7·5, of cane sugar 1·6, and of gum ·029; or, again, the quantity of salt which dialyses being 5·2, that of dextrin is ·034, of gum ·013, of caramel ·009, and of albumen ·005; whilst gelatin, extract of meat, and boiled starch, do not dialyse at all. The rate of dialysis is influenced by the depth of the fluid in the tray, by the area of the membrane, by the strength of the solution, and, to a certain degree, though less than liquid diffusion, by temperature. The process is not mechanical, but chemical, the results being more definite than those of liquid diffusion. Dialysis depends on the affinity of the substance experimented upon, for

the water in the moist permeable membrane. Crystalloids, which dialyse rapidly, have an affinity for, or unite with, the water of the septum, and, by successive combinations of their molecules with the water in that membrane, they pass through to the water outside it, and thus a movement, otherwise invisible, becomes apparent. On the other hand, colloids have little or no affinity for the water of the septum, and, therefore, do not make their way through it. The membranous septum is itself colloidal; its molecules have, therefore, only a slight affinity for water, and permit the stronger affinity of the crystalloids, successively to displace them, and so to pass through; whilst colloids generally, are too feeble to accomplish this displacement. Thin layers of any colloidal substance, such as films of gelatinised starch, albumen, jelly, gum, and mucus, also act as dialysers.

Dialysis has been employed for the artificial separation of crystalloids and colloids. Saline and earthy matters, rendered soluble by acetic or hydrochloric acids, may be dialysed from albumen, or lime from solutions of gum, pure albumen or gummie acid remaining. Morphia, strychnia, and other crystallisable alkaloids, have been separated from organic fluids; and even $\frac{1}{10000}$ part of arsenious acid, mixed with porter, milk, defibrinated blood, or pieces of intestine, has yielded 80 or 90 per cent. of that minute quantity, by dialysis, in 24 hours. These dialytic actions also explain more completely, the long known phenomena of endosmosis and exosmosis. The force concerned in liquid diffusion was at first named, by Graham, *osmotic* force; and endosmosis and exosmosis were regarded, by him, as due to the action of this force in opposite directions, or to a positive and negative osmosis; the direction of the chief visible current appears to be always towards any substance having the properties of a base, water flowing towards a salt, and from an acid. Subsequently, however, Graham distinguished liquid diffusion from diffusion through membranes, or dialysis.

Dialysis must take place in the living body, in which compound and simple permeable and colloidal membranes abound, such as the basement membranes, capillary walls, and cell walls, all of which are subject to the constant action of solutions of crystalloid and colloid bodies, either acids, alkalis, and salts, or albuminoid and extractive substances. The process of absorption most obviously suggests diffusive and dialytic actions; but so also do those of nutrition, secretion, and excretion, and even the interchange of the gases of the blood and air, in respiration, for these gases are dissolved at the moment of interchange. Moreover, the sapidity of crystalloids and the insipidity of colloids are associated respectively, with a high and a low diffusibility. It has even been suggested, as indeed was hinted by Dutrochet, that rapid dialytic action may take place, not only in vegetable movements, but also in the intimate changes of condition of the muscular fibres, in the states of contraction and relaxation, and that it may thus form a link in the transformation of chemical into mechanical force, which is realised in animal motion. Lastly, organisation and living action are indissolubly associated with the existence of one at least of these two great classes of substances, discriminated by their different dialytic power; for all the tissues of plants, and animals, from those of the seed or germ, upwards, are colloidal in their nature.

General Absorption.

The chief natural absorbing surface is the mucous membrane of the alimentary canal. Thus, it takes up the greater part of the food; moreover, saline, colouring, odorous, sapid, and other substances, may be detected, soon after having been swallowed, not merely in the blood, but in the secretions of distant glands; and, lastly, specific effects, medicinal or poisonous, may be produced upon remote parts of the system, e.g. upon the brain and spinal cord, as when prussic acid is applied to the tongue, strychnine is taken by the stomach, or nicotine is administered in enemata.

The mucous membrane lining the air-passages and air-cells of the lungs, is also absorbent, that of the air-cells especially taking up gases in a state of solution. Water, various other fluids, and saline solutions, accidentally introduced into the air-passages, are also partly absorbed. From certain cases of increase in the weight of the body, beyond that of the food and beverage taken, it has been inferred, though this is doubtful, that the pulmonary mucous membrane may even absorb the vapour of water from the air, instead of exhaling it, as it usually does. Many substances, of a more or less volatile or soluble character, may be introduced into the system through the air we breathe, either in a vaporous state, as in the case of carburetted, sulphuretted, phosphuretted, and arseniuretted hydrogen, cyanogen, alcohol, ether, chloroform, mercury, phosphorus, and miasmatic and contagious exhalations, or in the condition of fine particles, as e.g. arsenic. The general anæsthesia produced by chloroform, depends on its absorption by the pulmonary capillaries. Mercury and phosphorus, employed by the looking-glass manufacturers and lucifer-match makers, are taken up, partly by the mouth, but also probably by the lungs; and numerous cases of poisoning by arsenic, in which the health has been seriously deranged, have been observed amongst manufacturers of artificial flowers and green paper-hangings, from the arsenite of copper, or Scheele's green, employed by them. Such papers are unfit for dwelling rooms.

The conjunctiva is also absorbent, as is shown by the poisonous effects of prussic acid, dropped into the eye of a rabbit. Other mucous membranes likewise absorb fluids and dissolved substances; the bile, for example, becomes more or less inspissated in the gall-bladder.

Absorption by the skin also takes place, especially when a substance is kept in prolonged contact with it, as in the case of painters who do not cleanse their hands from white lead, and are attacked with the dropped wrist or paralysis of the extensor muscles of the fore-arm. In the thin and moist skinned *Amphibia*, absorption by the integument is very active; for if kept in a condition of drought, these animals become extremely attenuated; whilst they rapidly swell out, if then placed in a moist atmosphere, or upon damp earth, thus proving that their skin is both absorbent and exhalant. A dog placed in an air-tight vessel, with its head unenclosed, has been killed by the vapour of the oil of bitter almonds absorbed only through the skin. In regard to Man, absorption through the skin, if this be whole, is not very active; indeed, it has been, though erroneously, denied. The non-vascular cuticle impedes this process, and, in this way, is of great importance, especially in the practice of certain arts, in which the body is subject to contact with deleterious agents. Nevertheless, water may be absorbed by the whole skin, for the weight of the body is increased after the use of warm baths. (Madden.) Shipwrecked sailors, destitute of fresh water, find that, by immersion in the sea, or by wetting the clothes in sea-water, thirst is relieved; this may be partly attributable to a diminution of the exhalation of water from the blood through the skin, owing to the prevention of evaporation, but it is doubtless partly also due to direct absorption. In the use of very hot baths, above the temperature of the blood, more water is lost, by perspiration and pulmonary exhalation, than is absorbed, so that the body is lighter after such a bath; in a bath of 90° , the processes of absorption and exhalation are balanced, no change taking place in the body weight; in tepid and cold baths, cutaneous absorption exceeds exhalation, and the body gains in weight. Saline substances, such as iodide of potassium, cyanide of potassium, nitrate of potash, or chloride of ammonium, dissolved in baths, do not, according to some, enter the system; but others allege that they may be found in the blood and urine. The use of medicinal baths is based on the supposition that they are so absorbed; and the discrepancies between the results of different experiments, may, in part, depend on the employment of baths at different temperatures, which, as just stated, produce different results. A condition of exhaustion favours cutaneous absorption. The softening of the cuticle

greatly facilitates the process: thus, an onion crushed and worn in the shoe, will cause the breath to smell; garlic-poultices applied to the arm, and lint dipped in turpentine to the body, produce characteristic odours in the urine; jalap poultices may have an aperient effect; whilst applications of belladonna to the skin have been followed by dryness of the throat, dimness of sight, and by alarming, sometimes fatal, symptoms of poisoning. The introduction of foreign substances through the skin is greatly aided by the thinness of the cuticle and by friction, as is illustrated by the effects on the system of mercurial inunction, and also by the rubbing in and consequent absorption of cod-liver oil; but both these substances are absorbable even without friction.

The importance of the non-vascular cuticle as a protective covering, antagonistic to absorption, is shown indirectly by the effects of its removal; thus, the surface of the true skin, exposed in blisters, absorbs with great facility and rapidity; the unprotected and highly vascular surface of the cutis is no longer able to resist the entrance of the most deleterious substances; and even the cantharidin, or active principle of the Spanish-fly, used for producing the blister, is itself, sometimes, in this way absorbed. It has been stated that the lymphatics of the skin, which are very numerous and large, and have very thin walls, absorb adventitious substances, perhaps, more readily than the bloodvessels; the reverse, however, is the case with the lacteals.

The *serous* and *synovial* membranes also absorb, sometimes even very rapidly. Poisons injected into the pleural and peritoneal cavities, in living animals, are found to be most quickly taken up. Moreover, the serous exudations which occur in inflammation of these membranes, into the pericardial, pleural, and peritoneal cavities, are more or less rapidly removed by the curative process of *resorption*; the fluids poured out into the joints, in cases of rheumatic or other inflammation, and even blood extravasated into those cavities, are also, though more slowly, absorbed. The rapid absorption of the cerebro-spinal fluid (vol. i. p. 295) affords another instance of the facility of absorption from an internal cavity; so likewise does the absorption of blood and other effused matters, and even that of the broken and non-dissolved cataractous lens from the interior of the eyeball.

Absorption from the areolar connective tissue is proved by the taking up, from its interspaces, of dropsical fluids, or effused

blood; also by the poisonous effects of agents introduced experimentally into the areolar tissue in animals; and lastly, by the effects of the hypodermic or subcutaneous injection of solutions of morphia, or other medicinal agents, into the living human body, for the relief of neuralgic pain, and of the suffering after severe operations, or for the purpose of inducing sleep, or of relieving obstinate cough, or other irritation.

Lastly, absorption from the artificial surfaces of *ulcers* and *wounds*, is shown by the taking up of medicinal or poisonous substances, such as mercury, arsenic, morphia, atropine, conium, and other substances, applied to granulating sores.

The *vessels* concerned in general absorption in the vascular tissues, are the bloodvessels and lymphatics; but in the non-vascular tissues, as well as in non-vascular animals, absorption must take place by direct permeation into the cells or other tissue elements.

Absorption by the veins, or *venous absorption*, is proved by cutting across the limb of an animal, excepting its chief artery and vein, and then applying strychnine below the place of section, when the poison will still act, being conveyed in the blood of the undivided vein. Poisoning still takes place, if the artery and vein be also divided, and then rejoined by pieces of quill, so that the poison cannot be imbibed and conveyed by the coats of the vessels, but can only pass along the venous blood current. To show that the poisoning does not take place through the nerves, all parts of a limb may be divided, excepting the chief nerve, when poison, applied to it, does not affect the animal. Absorption by the veins generally, has also been proved by blistering the skin, applying a solution of ferro-cyanide of potassium, and, after a time, examining the blood in the veins, when that salt has been detected in it. Absorption also occurs through the portal veins. The pulmonary veins likewise absorb; for prussiate of potash, in solution, introduced into the trachea, appears sooner in the left cavities of the heart, to which the blood returns from the lungs, than in the right cavities, to which the blood returns from the body generally. Absorption by the pulmonary vessels also takes place in the passage of dissolved oxygen into the blood during respiration.

In absorption by the bloodvessels, the dissolved substance passes through the thin walls of the capillaries, or finest venules, and so enters the circulation; but as these vessels are always covered by tissue, sometimes exceedingly thin, as

in the air-cells, and sometimes thicker, as in the cutis, the absorbed substances not only pass through the coats of the vessels, but must also permeate this overlying tissue. This part of the absorptive process, corresponds with that form of absorption which occurs in the non-vascular tissues and in animals destitute of vessels. Absorption never takes place through the open mouths of vessels, as was formerly supposed; but, instead, a process of permeation occurs through the living tissues, physically identical with that of dialysis through dead animal and other moist permeable membranes, out of the body. This permeation is determined generally, first, by the tendency of different solutions to mix together, or of certain substances contained in the fluid on one side of the membrane, to pass into the fluid on the other side, which does not contain them; and, secondly, by certain chemical relations between the membrane and the substances applied to it, so that the membrane will permit some things to pass through it more readily than others. The rapid dialysis of acids, salt, sugar, and other substances, as proved by their quick production of flavour in the mouth, and the equally rapid passage of saline and metallic poisons, especially of the vegetable alkaloids, cyanide of potassium, prussic acid, and many other foreign and noxious substances, into the blood, corresponds with their crystalloid character; whilst the inert colloidal gum, and albumen, are slowly absorbed, and are almost tasteless. The removal of the dialysed material, from beyond the septum, increases the rapidity of the process; and thus also, the natural process of absorption is more rapid, the quicker the circulation in a part; for the constant renewal of the blood keeps up the required difference between that fluid and the solution of the foreign material, and the quicker the circulation the more rapid and complete is the renewal of the blood.

Absorption by the bloodvessels is necessarily favoured by the thinness of the layer of tissue which covers them, and is opposed by a thicker and denser covering; thus, absorption is very rapid from the lungs and peritoneum, quick also from the gastric and intestinal mucous membrane, not quite so quick from the exposed surface of the cutis, whilst it is almost entirely arrested, when this is covered by the cuticle. It is very rapid from the subcutaneous cellular tissue, where solutions injected artificially, come into almost immediate contact with the walls of the capillaries and venules. Absorption takes

place, though slowly, through the coats of even the larger veins, as has been shown, by exposing and insulating such a vein in an animal, and placing poison upon it, when death has followed. Absorption is favoured by moderate temperatures, but is retarded by temperatures much higher, or much lower, than that of the blood.

The rate of absorption of certain substances is very rapid; ferro-cyanide of potassium introduced into the stomach, has been found in the urinary excretion after the short space of 60 seconds; but when the stomach is more or less full, the absorption is retarded accordingly. (Erichsen.) The rapid passage of saline substances into the saliva, has been shown by Bernard. Alcohol is absorbed so quickly, that its effects on the brain, when injected into the stomach of dogs, are almost immediate, death occurring in about two minutes, the stomach being then found to be empty, and the blood to contain large quantities of alcohol. (Percy.)

Substances once introduced into the veins, by absorption, are carried with the blood to the heart, and thence, along the arteries to every part of the body. The condition of the circulation materially affects the rapidity of absorption. If the vessels be full of blood, or even if they be artificially injected with water, it is found that water introduced into the pleura is absorbed more slowly (Magendie); if the vessels be emptied by previous venesection, absorption takes place more rapidly. Absorption is also more active, when the water of the body has been diminished, by abstinence from fluids, or by unusual excretion. It is often suggested, that persons about to expose themselves to contagion or malaria, should previously take food, so as to diminish the chances of absorption, which is believed to be more likely to occur when the bloodvessels are in a comparatively empty state, or when the system is imperfectly nourished. The supposed immunity may be due to the less exhausted condition of the nervous system, or to some other unrecognized power of resisting diseased influences.

The process of absorption by the bloodvessels, is so dependent upon the movement of the blood, that if a ligature be placed on those vessels in the limb of an animal, or entirely around the limb, either, in the former case, absorption takes place slowly through the lymphatic vessels only, or, in the latter case, it does not occur at all. Thus, if a poison be inserted under the skin of an animal's foot, and a tight bandage be applied round the limb, no symptoms of general poisoning

ensue; but if the bandage be then removed, and the circulation through the limb be restored by gentle friction, poisoning, or even death will occur. Hence, the immediate ligature of a limb *above* a wound inflicted by a poisonous serpent, will arrest the further entrance of the venom into the circulation. The application of cupping glasses to a poisoned wound, operates, not merely by drawing out portions of the poison, owing to the removal of atmospheric pressure from the part, but also by stagnating the circulation in the injured and adjacent parts; sucking a poisoned wound acts in a similar manner. In a certain degree, the destruction of the part by caustic or the actual cautery also operates thus, but also by the simultaneous destruction of the poison itself. The prompt removal of the poisoned tissues also arrests further absorption.

The process of absorption is influenced by the nervous system, for, after division of the sciatic nerve in the hind limb of a guinea-pig, aconite, which was not previously taken up through the skin, has been found to be absorbed; this has been attributed to the dilatation of the smaller arteries, which follows section of the vasi-motor nerves. (Waller.) Certain stimulating agents, such as chloroform and turpentine, which favour absorption, may do so, by producing dilatation of the bloodvessels, as is indicated by the increased redness of the surface to which they are applied. It has been supposed that galvanism promotes absorption, but the contrary seems to be the case. Heat, friction, and moisture, as well as exercise of a part, obviously favour absorption; whilst the opposite conditions of cold, rest, and absolute dryness, disqualify a part from performing this function.

The share of the process of general absorption, due to the absorbent vessels, i.e. to *lymphatic absorption*, is small. When the cuticle of an animal is removed by blistering, and a solution of ferro-cyanide of potassium is applied to the denuded cutis, though the poison may be found in the veins, it has not been detected in the thoracic duct. Nevertheless, even when the abdominal aorta and inferior vena cava of an animal have been tied, to prevent the circulation of the blood through the hinder limbs, and when, in addition to this, the internal iliac veins have also been tied, to cut off the collateral circulation through the veins of the pelvis, cyanide of potassium, and strychnine, inserted beneath the skin of the feet, even after the limbs have become rigid, have been detected above the seat of the ligatures, and have produced characteristic symptoms of poison-

ing; the lymphatic vessels must here have been the channels of absorption. In certain instances, morbid products are conveyed through lymphatic vessels, as, e.g. decomposed animal fluids, pus, simple or specific, and also cancerous matter; but the extension of disease along the course of the lymphatics, and through the lymphatic glands, may be sometimes due to the propagation of a morbid process in the coats of the lymphatics. The colouring matter of the bile has been seen in the lymphatics of the gall-bladder, after ligature of the gall-duct, and consequent retention of the bile in its receptacle. The subcutaneous lymphatics near tattooed portions of the skin, are sometimes found charged with colouring matter, forming characteristic ramified lines, differing in course from that of the bloodvessels. Moreover, the identity of structure between the lymphatics and the lacteals, and the undoubted absorbent function of the latter, favour the conclusion that the former vessels likewise absorb. The termination of all the lymphatics in the venous system, and the direction of the valves in their interior, not only support this view, but enable us to determine the course and destination of their contents.

The *lymph*, elsewhere described (vol. i. p. 67), resembles chyle deprived of its molecular basis, and of nearly all its fatty matter; but its clear, colourless, and limpid character, so unlike the milky opalescent aspect of the chyle, renders it difficult of detection in its vessels during life. Distended transparent lymphatics have, however, been seen on the surface of the liver in recently killed animals, and the lymph itself has been observed flowing from the cut surface of that organ, and also from lymphatic fistulæ, the result of disease in man, and from artificial openings established in the lymphatics of a horse's leg.

The constituents of the chyle are derived essentially from the digested food, but the precise source of the lymph contained in the lymphatics, and also in the lacteals, during the intervals between digestion, is not perfectly understood. In part, the lymph would seem, from its similarity in composition, to be derived from the nutritive plasma, which permeates all the living tissues. This plasma, itself derived from the liquor sanguinis, consists chiefly of that part of the nutrient fluid poured out through the walls of the capillaries, which is not employed for the nutrition of the tissues. The surplus of nutrient materials, together with sufficient water, is supposed to pass into the lymphatics in the form of lymph, and so to be

ultimately returned to the blood. It is also supposed that the tissues, themselves undergoing nutrient changes, yield products which may, in part, be fitted to enter the commencing lymphatics; but these, no doubt, chiefly find their way into the capillaries and minute venules, and thus entering the blood, are subsequently cast off as excretory products. Whatever be its source, the fluid and dissolved constituents of the lymph find their way into the commencing lymphatics, through the delicate coats of these vessels, which form closed tubes, having no open mouths, and no direct communication with the capillary or other bloodvessels. It has, however, been recently maintained, that the commencing lymphatics communicate with, or originate in, lacunar spaces, situated in the areolar tissue which pervades the whole body, and that they commence in fine hollow processes in the ramified nuclear fibre cells of that tissue, which are also supposed to be hollow. But these views have not been confirmed.

As the commencing lymphatics are generally most abundant in tissues in which the nutritive changes are not very active, and least abundant, or not detected, in organs which undergo very rapid metamorphosis, it is probable that the waste products of nutrition are chiefly, or, in the case of the nervous centres, entirely, returned into the circulation, through the capillaries and minute veins. It is probably correct to infer that the lymphatics do not remove wasted and excrementitious materials, unfit for the further use of the system, as Hunter formerly supposed, but rather that they take up matters which may be again employed in the blood, for the purposes of nutrition. The fibrin of the lymph, which enables that fluid to form a slight coagulum, though not in the vessels, as occurs with the blood, and also the lymph-corpuscles, which so closely resemble the white corpuscles of the blood, are present before the lymph has passed the lymphatic glands, but they increase in quantity beyond those glands. The fibrin may be partly derived from that portion of the nutritive plasma effused through the walls of the capillaries, which is absorbed by the commencing lymphatics; its gradual increase in quantity in the larger lymphatics may depend on inspissation, or enrichment, taking place within the glands, which are very vascular; additional *fibrin* or *fibrinogen*, from which the fibrin is formed, may even be elaborated in these glands. The lymph corpuscles may also be, in some way, more abundantly developed within the glands, which must, more or

less, retard the rate of motion of the lymph. The outer areolar spaces of the glands, which receive the lymph as it enters, contain numerous corpuscles and granules, some of which are probably added to the moving stream of lymph. But such corpuscles are undoubtedly formed, though in smaller number, independently of the glands; for they may be detected in both the lymphatic and lacteal vessels, *before* these have passed through glands; also in the lymphatic vessels of the hind limbs of birds, on which no lymphatic glands are found; and likewise, in the lymph of Reptiles, Amphibia, and Fishes, although in these animals no lymphatic glands exist at all, but only complex or simple lymphatic plexuses. The destination of the lymph corpuscles is the blood; they probably constitute in the Vertebrata, after birth, the chief, if not the only source of the white corpuscles of the blood, as will again be mentioned in the Section on Sanguification.

Absorption of the Food.

The absorption of the digested food is only a special example of the general absorptive function. It has been maintained by some, that the nutritive constituents of the food, are absorbed from the alimentary canal by the *lacteals* only; by others, that this absorption is accomplished by the minute *blood-vessels* alone; but both sets of vessels are concerned in this function, each apparently performing special offices.

That the *bloodvessels* of the alimentary canal absorb, has been thus proved. Strychnine has been introduced, in a living animal, into a portion of intestine, included between two ligatures, and separated from the mesentery, excepting by its arteries and veins; so long as the circulation through the intestine is arrested by compression of the bloodvessels, no symptoms of poisoning occur, but when the blood is allowed to flow through the vessels, the animal is speedily poisoned. Moreover, certain alimentary substances, such as albuminose, dextrin, sugar, and lactic acid, have been found in the blood of the mesenteric veins; many chemical substances, especially metallic salts, and those which easily penetrate animal membranes, as e.g. the ferro-cyanide of potassium, when taken with the food, have been detected in the venous blood, and even in the secretions; so also odorous substances, such as musk, camphor and garlic, alcohol, and soluble colouring matters, as e.g. cochineal and madder, taken into the stomach,

have been found in the blood. Even *insoluble* substances, such as charcoal, sulphur, and, it is said, starch, taken internally, in a state of minute subdivision, have been detected in the mesenteric veins.

The entrance of nutrient and other matters from the intestinal canal into the *lacteals*, is proved by the distension of those vessels with white chyle, during digestion, especially after ligature of the thoracic duct. The chemical composition of the chyle (vol. i. p. 92), shows that, besides absorbing the water of the food, the lacteals take up small quantities of saline substances and extractives, a certain quantity of the albuminose products of digestion, and, in particular, a very large amount of fatty matter. With regard to non-nutrient substances, however, the absorptive power of the lacteals, is much more limited than that of the veins. First, with regard to poisons : in experiments, the opposite of that just recorded, the arteries and veins of a piece of intestine, isolated by two ligatures, have been tied, whilst the rest of the mesentery, containing the lacteal vessels, has been left untouched ; poison then introduced into the intestine, is not absorbed, so as to destroy the animal, until, by loosening the threads on the bloodvessels, blood is again allowed to flow through them. (Magendie and Segalas.) To such experiments it has been objected, that tying the bloodvessels suspends the functions of the lacteals, which may lose their absorbing power, when the capillary circulation around them is stopped. The experiment has, therefore, been varied, so as to permit the local circulation to continue ; thus, the vein from the part of the intestine into which the poison is introduced, is first compressed, and then opened below the point of compression, so that the blood returning along it, escapes, and does not enter the general circulation, although the local circulation in the intestine still goes on. Under these conditions, no poisoning takes place, but this speedily happens when the pressure on the vein is removed, and the blood returning by it, enters the general circulation. Nevertheless, poisons are slightly and slowly absorbable by the lacteals, especially poisonous salts in a state of solution. The lacteals also absorb innocuous saline matters, sugar, and extractive matters, but not so easily as the veins ; neither do they so readily take up odorous substances ; with regard to soluble colouring matters, turmeric is taken up by them, whilst other dissolved colouring substances, such as madder-lake, indigo, gamboge, and rhubarb, are said not to

be absorbed. (Tiedemann and Gmelin.) Substances in a state of extremely minute subdivision, such as charcoal, sulphur, and even particles of indigo, have also been found in the lacteal vessels, as well as in the bloodvessels, having probably penetrated into those vessels in the villi.

From the preceding facts, it would seem that the absorbing power of the veins is *general*, whilst that of the lacteals is *select*. The veins permit the entrance into them indifferently, of probably all kinds of *soluble* substances, which do not actually alter or destroy the texture of their coats, but the lacteals have a sort of selective power, by which they take up certain substances in preference to others, nearly, or completely, rejecting some. Both kinds of vessels, but especially the lacteals, appear to allow, in some way or other, the entrance into them of exceedingly minute particles of insoluble substances, not by a process of dialysis, but by *porous diffusion*, the pores being, however, invisible in the walls of the capillaries or lacteals, though specially discernible, according to some, in the epithelial cells upon the villi. The direct penetration of the walls of the capillaries and lacteals, has been compared with that of a needle entering a larger vessel. A certain hardness of the penetrating particles is necessary, for lamp-black, which is finer and softer than charcoal, does not enter the vessels. Penetration of the soft tissues, by minute bodies, without serious injury to the former, is illustrated by the wandering movements of the smaller Entozoa, through and amongst the living tissues.

By far the larger quantity of the water of the food and drink, and of the saliva and gastric juice, is taken up by the veins. This process begins immediately, and goes on rapidly, in the stomach; it regulates the consistence of the gastric contents, and the strength and acidity of the gastric juice; more water, including some of that belonging to the biliary, pancreatic, and intestinal secretions, is taken up by the veins of the intestines; but much is here absorbed by the lacteals, to form the fluid part of the chyle. The saline constituents of the food are absorbed directly, in chief part, by the veins, these substances, such as chloride of sodium and phosphate of soda, requiring, like water, no digestion; minute traces of them, however, also enter the lacteals. Sugar and extractive matters likewise enter chiefly by the veins, and but slightly through the lacteals. The organic acids, and their salts, are converted into carbonates, and undergo venous absorption. Alcohol also

passes in chiefly, if not entirely, by the veins, and so likewise do the ethereal, odorous, sapid, and colouring matters of the food, and probably also most medicinal and poisonous substances. Venous absorption even begins in the mouth, as may be inferred from the occurrence of taste; but it is much more active in the stomach and intestines. Soluble albuminoid substances, if not converted into albuminose, may be absorbed directly by the veins of the stomach and small intestine, and certainly by those of the large intestine, as is exemplified in the restorative effects of nutrient enemata. The soluble albuminose, the product of digested albuminoid bodies, must also be in part absorbed by the veins; for the quantity of albumen taken up into the chyle, is scarcely equal to that contained in the food. The gelatin-peptone probably enters the veins. Lastly, fatty matters have not been directly proved to be taken up by the veins, though, if in a saponified condition, they may be so, and the capillary network has been seen to assume a turbid appearance, as if containing fat. (Brücke.) Besides this, in cases of disease, not only the colouring substances, but the fatty matters of the bile, enter the circulation through the venous system. The chief channels of entrance of the fatty matters emulsified during the process of digestion, are, however, the lacteal vessels, as is proved by the large proportion of fat in the chyle.

The veins, thus, absorb most of the water, and of the saline, saccharine, extractive, acid, alcoholic, odorous, sapid, and colouring substances, together with some albumen or albuminose, probably the gelatin peptone, and possibly saponified fatty matters. On the other hand, the lacteals absorb the rest of the water, small quantities of the saline, saccharine, and extractive substances, a considerable proportion of the albuminose bodies, and nearly all the fat. In the intervals between the absorption of food, the lacteals of the small intestine, like the lymphatics of other parts of the body, contain only a transparent lymph, and then perform, for the tissues of the intestine, the office of the lymphatics generally. The same is true, at all times, of the lymphatics of the stomach and of the large intestine, which never contain chyle, but always lymph.

It may be presumed, that the absorption which takes place from the stomach, is chiefly performed by means of the blood-vessels, because the gastric mucous membrane is destitute of villi, and, therefore, of proper lacteal vessels; nevertheless, nutrient and other substances, prevented from entering the

intestine, by ligature of the pylorus, have been shown to be absorbed by the gastric lymphatics. The process by which certain parts of the food are absorbed by the *bloodvessels* of the alimentary canal, must be identical with that of the general absorption of soluble substances from other vascular surfaces, or tissues, of the body. Like the latter, it partakes of the nature of the physical processes of liquid diffusion and dialysis. Water, and substances dissolved in it, such as soluble salts, sugar, extractive matters, and soluble albumen or albuminose, permeate the epithelial and subjacent layers of the mucous membrane, and also the thin coats of the capillaries and smallest venules, not merely of the villi, but of the general surface of the intestinal canal, in the same manner, probably, as a similar solution would pass through moist dead animal membranes. The temperature of the interior of the body, greatly favours the osmotic process. The penetration of the water with its dissolved contents, is a dialytic phenomenon; and by a similar action, the entrance of certain substances is probably permitted more readily than that of others, the crystalloid substances, such as the salts and sugar, with the creatin and creatinin of the extractive matters, and also the albuminose and gelatin peptones, entering more readily than the colloid substances, such as dissolved starch, mucilage, albumen, gelatin, and the non-crystallisable extractive matters. But dissolved colloidal starch is converted by the salivin, into the crystalloid sugar; and albumen and gelatin, when digested by the acid pepsin, are changed into albuminose and gelatin peptones, which, though not true crystalloids, are much more dialysable than the albuminoid and gelatinoid substances contained in our food. The molecular metastases, or changes in question, may be in some way connected with a process of *hydration*. It has also been suggested that a colloid body may be formed by groups of crystalloids, and so its temporary metastasis from one condition to another, may be explained. It is possible also that there may be special reactions between alimentary substances and the living mucous membrane and walls of the vessels, favouring or resisting the passage of some or other of those substances. But this is uncertain; and the act of absorption by the bloodvessels, is so easy, rapid, and general, in the case of non-nutrient, and even of many poisonous substances, that their walls can possess but little if any power of selection or exclusion. Fatty matters, however, unless in a state of saponification, do not readily, or at all,

enter the bloodvessels. Experiment has shown that even when finely divided, as they exist, for example, in the yolk of the egg, and in milk, they may be made, under moderate pressure, to permeate moist membranes (Heidenhain); and further, that the natural repugnance between oil and wetted membranes, is much overcome, if these latter are saturated in alkaline solutions or in bile. (Wistinghausen.) A temperature of 100° , or that of the interior of the body, facilitates this permeation of fat. Though acids generally, and especially the hydrochloric acid, which exists in gastric juice, are rapid dialysers, and so penetrate very quickly the colloidal albuminoids of the food, which they help to dissolve, yet acidity appears to be opposed to the absorption not only of fat, but of actually dissolved substances; whilst, a neutral or alkaline condition favours their absorption. In certain cases, especially in regard to organic substances of an extraneous, medicinal or poisonous, character, it appears that the digestive fluids not only dissolve, but also alter, the properties of substances taken into the stomach. Thus, there are two substances found together in the bitter almond, named *amygdalin* and *emulsin*, the former of which is decomposed by a catalytic action of the latter, and gives rise to the formation of prussic acid. Now, it has been found by Bernard, that amygdalin, introduced by itself into the stomach of any animal, is digested, dissolved, and absorbed, without giving rise to poisonous symptoms. Again, emulsin alone taken into the stomach, produces no ill effects. If, however, after the absorption of the dissolved amygdalin from the stomach, emulsin be directly injected into a vein, death speedily ensues, from the formation of prussic acid in the blood or tissues, by the decomposition of the dissolved amygdalin under the influence of the emulsin, thus introduced into the circulation, and brought into relation with it. But on the other hand, if the emulsin be introduced into the stomach, and the amygdalin be injected into the bloodvessels, poisoning does not ensue, showing either that the emulsin is not absorbed from the alimentary canal, or that its properties are destroyed. The latter is, probably, the case, for emulsin is easily soluble, and when it and the amygdalin are introduced together into a vein, or even into distant parts of the circulation, their meeting in the blood is immediately followed by the characteristic decomposition of the one under the influence of the other, prussic acid being evolved, and the animal being killed.

After the absorbed materials have entered through the capillary walls, their onward progress depends upon the forces concerned in the circulation of the blood.

The process of absorption by the *lacteals*, is of a more special nature than that by the bloodvessels; for though they admit the entrance, probably by simple dialysis, of water, with traces of saline, saccharine, and extractive substances, that is, of the crystalloid bodies, and also take up in certain proportion, the dialysable albuminose, yet they are specially characterised by absorbing fatty matters, which, though crystalloid, are insoluble in water, and non-dialysable, unless they are actually saponified. In the alimentary canal, however, they are merely liquefied, or emulsified, *i.e.* reduced to a state of extreme molecular subdivision, or they are decomposed into their fatty acids and glycerin. The special power of the lacteals, of absorbing fatty matters, has not yet been fully explained. Some have supposed that the fats pass through the epithelial substance of the villi, into the lacteals, in a state of saponification and solution, and then reappear as neutral fats in the chyle. The action of the bile and of the alkaline pancreatic and intestinal juices, as already explained, undoubtedly prepares the fatty matters for more easy penetration into the lacteals. The epithelial cells of the villi, which are often found distended with drops of fat during the digestive process, are probably specially concerned in the absorption of fat by the lacteals. It has been supposed that these cells feed, as it were, upon the fatty matters contained in the intestine, and, having become distended, discharge their fatty contents into the commencing lacteals. A nutritive process is imagined to take place, similar to that which occurs in the epithelial cells lining the commencing ducts of the secreting glands, but in a *reverse* direction; that is to say, not by the assimilation of materials from the blood into these secreting cells, to be discharged at the surface, but by the assimilation of materials from the surface inwards, to be discharged into the lacteals. This fatty matter must enter the epithelial cells covering the villi, in the form of exceedingly minute molecules, by porous diffusion or transmission; and the fine vertical lines or streaks, noticed by certain observers in these cells (p. 158), are supposed, by some to be minute pores or channels, through which the highly subdivided fatty matters, or even fine solid particles of charcoal, enter the interior of the cells, and so proceed into the lacteals. How the fat particles pass from the

cells into the commencing lacteals, is not known. By some it is said that the inner pointed ends of the epithelial cells, terminate in caudate areolar tissue cells, which, in their turn, communicate with the lacteals. But this is more than doubtful; and the actual transmission is probably by porous diffusion, through true but invisible pores.

The onward motion of the chyle, from the commencing lacteals in the villi, into and through the larger absorbent vessels on the walls of the intestine, and along the mesentery, to the thoracic duct, depends on several agencies. First, the chief cause is probably the *vis a tergo*, or *force from behind*, originating in the continuous nature of the absorptive process at the commencement of the lacteals. The existence of this force, is proved by the distension of the whole system of vessels, including the thoracic duct, even to the occurrence of rupture, when that duct is tied in an animal a short time after it has been fed. This pressure from behind, produces a motion of the fluid in the larger absorbents, just as the continuous absorption of fluid by the spongioles at the extremities of the roots of trees, causes the rising of the sap. Even in simple dialysis, in purely physical experiments, as with the endosmometer of Dutrochet, there is an ascending motion of the fluid in the graduated tube, due to the energy at work in the moist membrane. Secondly, the contraction of the non-striated muscular fibres of the villi, which, when stimulated by galvanism, in living animals, have been observed to shorten those processes, must compress the central lacteal of each villus, and so urge on its contents into the general network of absorbents. The bile may help to excite this muscular act. Thirdly, the contraction of the scattered muscular fibres in the submucous coat, and also the peristaltic movements of the proper muscular coat of the intestine, likewise excited by the food and by the bile, will serve to empty the intestinal lacteals into those of the mesentery. Fourthly, the lacteals and the lymphatics, as well as the thoracic duct, have muscular fibres in their coats, the contraction of which moves onwards their contents, and also empties them on their being exposed to the air, in animals recently fed; this explains the collapsed state of these vessels after death. There are also muscular fibres in the inter-alveolar septa of the lymphatic glands. Fifthly, the semilunar valves found in pairs in the interior of the larger lacteals, both in the walls of the intestine and in the mesentery, must determine the movement of the contained chyle, always in the

same direction, by whatever force such movement may be induced. In this way, even the pressure of the abdominal walls and viscera, must assist the onward flow of the chyle. Its direction necessarily coincides with that of the free margins of the valves, viz., towards the thoracic duct, all retrogression of the chyle in the direction of the intestine, being effectually prevented. Lastly, the quick motion of the blood in the great veins at the root of the neck, into which the thoracic duct opens, and the effects of inspiration, are also causes of a certain *vis a fronte*, or *force from before*, which draws the lymph or chyle from that duct into the veins. The descent of the diaphragm in inspiration, acts not only by removing pressure from the great veins in the thorax, but also by increasing the pressure on the abdominal lymphatics and the lower end of the thoracic duct.

The quantity of mixed lymph and chyle poured into the blood in twenty-four hours, has been estimated, from experiments in animals, to be, in an adult man, nearly 29 lbs., of which the smaller proportion is chyle, the rest being lymph. (Bidder and Schmidt.) It has been ingeniously suggested by Vierordt, that, if the absorption of fat be supposed to take place exclusively by the lacteals, and the composition of the chyle be assumed to be uniform, the daily quantity of chyle may be calculated from the daily quantity of fat taken in the food. Thus, the quantity of fat consumed in the day, being taken to be 3 oz., and the chyle, to contain three per cent. of fatty matters, the quantity of this fluid formed daily would be about 100 oz. or $6\frac{1}{4}$ lbs. The chyle is a highly nutrient fluid. It adds not only fatty matter, but, like the lymph, a certain amount of fibrin or fibrinogen, albumen, extractives, and salts, and also a number of granules and proper corpuscles, to the blood. The *gradual* entrance of these into the blood, is of some importance in the maintenance of the proper composition of that fluid, and, accordingly, nutrient substances are absorbed rather more slowly than those which are not nutrient. The more concentrated the products of digestion, however, the more rapid is their absorption; at least this is true of sugar and albuminose. (Becker, Funke.)

Intrinsic Absorption.

The special process, by which the fluid or solid parts of the living body, are interstitially removed, the so-called *intrinsic*

absorption, is usually described with the simpler phenomenon of general absorption. But it is a different and more complex process, implying a previous liquefaction, or fine disintegration, of the solid particles of the absorbed tissues, before these can enter the lymphatics or bloodvessels concerned in their removal. It is in part, therefore, a nutritive or *denutritive* process.

Intrinsic absorption is sometimes simply *interstitial*, accomplishing the removal of tissues, molecule by molecule, without any solution of continuity, or breach of substance, in them, the part affected becoming merely smaller, and not necessarily undergoing any special change of form. During simple interstitial absorption, nutritive changes, involving the deposition of fresh material, must still go on, but the process of absorption is relatively more active than that of the deposition of new matter. This kind of interstitial absorption is illustrated in the *wasting* which takes place as the result of hunger or starvation, and also in the disease known as *atrophy*.

Another form of intrinsic absorption, known as *progressive absorption*, involves more or less solution of continuity, or breach of substance. It is often apparently caused by pressure interfering with the nutrition of a part; it is exemplified in certain morbid processes, as when an aneurismal, or other deep-seated tumour, in approaching the surface, induces absorption of the interposed structures, even the bones being absorbed under the effects of constant pressure. Abscesses also tend to the surface of the body or of internal mucous cavities, by a similar progressive absorption. Another form of this process is named *disjunctive* absorption; in this, the living part of a tissue, in immediate connection with a dead portion, is removed by absorption, and so the dead part is detached; such a process occurs in the separation of a slough from a soft tissue, or of a necrosed or dead portion of a bone, from a living part, and also in the throwing off of a portion of the entire limb, as in the case of gangrene of the foot.

Certain tissues also undergo intrinsic absorption much more readily than others. Bone, one of the hardest tissues in the body, is very readily absorbed; its numerous Haversian canals, and cancelli, and even its general medullary cavities, are channels or spaces produced, during its growth, by an absorptive excavation of a previously solid osseous tissue; such changes occur in it, even when it is fully developed; and, as just now stated, it is very easily absorbed under abnormal pressure.

The fangs of the temporary or milk teeth, which are composed of dentine, a substance more compact than bone itself, undergo progressive absorption under the influence of pressure from the summits of the rising permanent teeth, and, in this way, are loosened, and finally drop away from the gum. Cartilage is less easily absorbed than bone, but, nevertheless, it does yield to that process. The fasciæ, areolar tissue, skin, and mucous membranes, also give way under the progressive absorption caused by abscesses which are advancing to the surface; the epidermis and epithelium, however, burst mechanically. Vascularity is necessary for the occurrence of true intrinsic or progressive absorption. Cartilage is probably absorbed by closely adjacent vessels. All vascular organs and tissues are liable to progressive absorption under pressure, and all may undergo waste or atrophy.

In the progress of development, in Man and animals, many instances occur of the disappearance of parts not permanently needed, such as the temporary gills of the higher Amphibia, the tails of the tadpoles of the anourous species, and also certain large bloodvessels which are no longer required in more advanced conditions of development. The removal of the membrane which closes the pupil of the eye, when it is no longer needed for the vascular supply of the lens, is another instance of intrinsic absorption; so also are the many changes which take place in the jaws, during the formation of the sockets for the teeth, and their filling up when these are lost. Sometimes an entire organ of complex structure, with its proper parenchyma, bloodvessels, lymphatics, and nerves, becomes atrophied by interstitial absorption. Thus, the *thymus* body, a ductless gland, which exists in the fore part of the neck and thorax, in the young of Man, and the Mammalia generally, disappears as life advances. In the human body, the thymus exists only as a mere vestige, after the age of twelve years.

By the process of *resorption*, blood, lymph, dropsical effusions, pus, and other fluids are easily taken up from the areolar tissue in which they are extravasated or effused. From the serous cavities, and especially from the joints, they are less easily resorbed. It is probable that the solid albuminoid constituents of such effused products, undergo a chemical change of degeneration, becoming converted into fatty matter, and some nitrogenous, perhaps ammoniacal, compound, both of which are absorbable. It has been found that a piece of

muscle introduced into the cavity of the peritoneum, first loses its water, and then gradually undergoes a fatty change.

When *inflammation* reaches a certain height, besides the exudation of plastic matter from the bloodvessels, and the formation of cells, which may end in the production of pus, or of new-formed tissue, the nutrition of the pre-existing tissue itself may suffer, and it may become slowly disintegrated, or undergo molecular death. It then falls away imperceptibly, and a chasm is left, called an *ulcer*, the process itself being named *ulceration*. Both the vascular and non-vascular tissues are liable to become ulcerated. It was once supposed that the formation of an ulcer, or the ulcerative process, began and continued by the interstitial absorption of an inflamed tissue, this form of absorption being named *ulcerative absorption*; but although a true absorptive process may occur in some forms of ulcer, there is little doubt that, generally speaking, the erosion of a living tissue, known as ulceration, is due to the molecular death and melting away of the tissues. Ulcers always occur on surfaces, whether in vascular parts, such as the skin, mucous membranes, and bones, or in non-vascular parts, such as the cornea and the articular cartilages.

There is reason to believe that both the *lymphatics* and the *bloodvessels* are concerned in the various forms of intrinsic absorption or resorption. The agency of the lymphatics is rather inferred from analogy, than demonstrated by facts. It is impossible to doubt that the bloodvessels are also concerned in it, for the phenomena may take place in parts in which lymphatics are not believed to exist, as, for example, in the brain; but the process is here undoubtedly much slower.

Intrinsic absorption is favoured by continued moderate pressure, as by the use of surgical bandages, which, however, may also act by restraining the supply of blood and the nutrition of a part. It is also favoured by an elevated position, by friction, and by stimulating applications. It serves important uses in the economy, enabling the whole system to be maintained, for a time, upon itself, and, by the absorption of fatty matter stored up in the adipose tissues, supporting the respiratory function, even in the absence of food. In the removal and casting out of diseased products, or dead parts, it also exercises a useful and conservative office.

In conclusion, it may be repeated that, in addition to these important uses, the function of absorption generally, ministers to the nutritive function, by the conveyance into

the circulating system, not only of the materials of the food, but also of the residual part of the plasma of the blood, not immediately employed in the nutrition of the tissues amongst which it is poured out; and, lastly, that it assists in the elaboration of those essential organised elements of the blood, its white and its red corpuscles.

The Absorbent System, and Absorption in Animals.

A lymphatic and lacteal apparatus exists only in the Vertebrate Subkingdom. In all cases, the finest vessels commence by blind extremities, and the absorbent trunks empty themselves ultimately into the veins, forming, as it were, a closed system superadded to, or constituting an offset from, the blood system, with which, in the lower Vertebrata, it communicates at a great number of points, not only in the neck, but also in the abdomen and pelvis.

In Mammalia generally, as in Man, well-developed lymphatic glands are found; in the Carnivora, owing probably to the shortness of the intestine, the mesenteric glands are so closely aggregated, as to appear like a large conglomerate gland. In Birds, lymphatic glands are also found, especially in the fore part of the body, but they are less perfectly developed, and, in other parts, are replaced by elaborate plexuses of lymphatic vessels; in accordance with the general lateral symmetry of these animals, there are two thoracic ducts, each with its receptaculum chyli; in certain birds, as in the goose, dilatations of the pelvic lymphatics are met with, the coats of which are provided with unstriped muscular fibres, which do not contract periodically or rhythmically; the lymphatics of the hinder part of the body communicate very frequently with the veins. In Reptiles, the lymphatic glands are absent, but their place is apparently supplied by the great size and abundance of the absorbents themselves, and by numerous plexuses of closely-packed vessels; the valves are either imperfect, or are found only in the larger trunks; communications with the veins, exist in the lower limbs. In this Class, as well as in the Amphibia and Fishes, there occur, connected with the lymphatic system, those remarkable rhythmically contractile sacs, known as *lymphatic hearts*; they have been found in the neck of certain Ophidia, and in the pelvis of the turtle and crocodile. In the Amphibia, the lymphatics are relatively large, but few in number; neither valves nor lymphatic glands exist; the lymphatic hearts, usually four in number, have walls composed of *striated* muscular fibres: in the frog, two of these hearts are situated, one on each side of the neck, opposite to the third cervical vertebra, and two posteriorly in the pelvic region. It is in Fishes that the absorbents are fewest in number; they are delicate transparent vessels, destitute of valves, excepting at the points of entrance into the veins, which are here very frequent: the lacteals appear almost destitute of distinct walls. In the tail of the eel, and in many fishes, behind the cranium, outside the jugular veins, there are found pairs of lymphatic hearts, or dilatations of a similar nature to the true lymphatic hearts of the Amphibia. No lymphatics have been observed in the amphioxus.

The chyle varies in colour and opacity in different animals ; thus, it is very milky-looking in the carnivorous, but almost colourless in the herbivorous Mammalia ; it is also more transparent in the cold than in the warm-blooded Vertebrata.

It is usually considered that no vessels homologous in character and office, with the lymphatics and lacteals of the Vertebrata exist in Non-vertebrate animals ; but it has been suggested that the so-called blood-system of the Mollusca and higher Annulosa, with its usually colourless contents, including corpuscles much more like the white than the red blood corpuscles of the Vertebrata, may possibly be the homologues of the vertebrate lymphatic system. Be this as it may, these vessels are undoubtedly concerned, not only in the function of circulation, but also in that of absorption ; for absorbed materials not only pass into the perivisceral cavity, and penetrate the soft tissues of the body, immediately and directly, but they also enter the interior of these so-called bloodvessels, mingle with the circulating fluid, and thus are conveyed to the most distant parts of the frame. Such vessels must be concerned both in the absorption of the food, and in all the phenomena of general extrinsic and intrinsic absorption. In those Non-vertebrate animals, which, as the Annuloida, possess the so-called water vascular system, or some analogous vessels, general absorption may be assisted by them. In the Cœlenterata, all of which are destitute of proper vessels, the fine tubular extensions of the body cavity into the soft disc, must aid in this process ; but in the simple hydra, absorption must be accomplished by direct imbibition through the cells lining the digestive cavity, and by general percolation through the soft intercellular spaces. In the Protozoa, it must occur through the sarcodous cell-substance, of which those animals consist.

Whilst, therefore, in the lowest non-vascular animals, nutrient matters at once permeate the tissues which they have to nourish, and whilst, in all animals possessed of vessels, whether absorbent or circulating, or fulfilling both functions, a similar permeation of nutrient matter takes place through the lining membrane of the digestive cavity, yet, in the latter case, it has no immediate nutrient action on the solid tissues, but speedily passes into the bloodvessels or absorbents, and thus directly or indirectly enters the circulating fluid or blood. Mixed with this, it probably undergoes further elaboration, before it again transudes through the walls of the fine vessels, into the solid tissues, which are ultimately nourished by it.

CIRCULATION.

We have seen that the absorbent vessels end in the great veins at the root of the neck, and that there, the lymph and chyle are poured into the blood. The blood is not permitted to remain stationary in any part of the living body ; but in order to fulfil its offices in the general functions of nutrition,

secretion, and excretion, and its special office of stimulation in regard to the nervous and muscular systems, and in order that it may be constantly purified by the respiratory process, it is kept in continual motion throughout the whole of life. This motion of the blood takes place, in Man and in most animals, in distinct cavities and channels, viz., through the heart and bloodvessels, the arteries, capillaries, and veins. The movement itself is named, from its definitely recurrent course, the *circulation of the blood*.

The general distribution of the arteries, capillaries, and veins of the body, and the structure of these vessels, have already been explained (vol. i. pp. 18 and 57). The heart, or central organ of the circulation, requires now to be described.

THE HEART.

The Heart and Bloodvessels.

The heart, enclosed in its sac, or pericardium, is placed obliquely in the thorax, between the lungs (fig. 13), occupying a space about 4 inches in width. It is of a conical shape. Its base, connected with the large bloodvessels, is directed upwards, backwards, and to the right, corresponding with the middle of the dorsal region; its apex turned downwards, forwards, and to the left, points to the left of the sternum, opposite the interspace between the fifth and sixth ribs, two inches below and one to the sternal side of, the left nipple.

Its anterior surface, turned slightly upwards, is convex; its posterior surface, directed downwards, and supported by the diaphragm, is flattened. This organ is about the size of the closed fist. In the adult male it weighs from 10 to 12 oz., but from 8 to 10 oz. only in the female. Its proportion to the body, in the former sex, is as 1 to 169; in the latter, as 1 to 149. It measures about 5 inches in length, $3\frac{1}{2}$ in width, and $2\frac{1}{2}$ in thickness. It increases in weight, and enlarges in all its dimensions, as life advances.

The heart is a hollow muscle, its cavity being completely divided internally, by a longitudinal septum, into a right and a left lateral chamber. Each chamber consists of two cavities, one called an *auricle*, the other a *ventricle*, marked off from each other by a transverse constriction, which forms on the surface the *auriculo-ventricular groove*. The auricle and ventricle of the same side open into each other, but those of

the opposite sides do not communicate. The two auricles are placed at the base of the heart; their walls are thin; they are separated from each other by the median septum, and receive blood from large veins. The two ventricles lie below the auricles, have walls of considerable thickness, and form the most solid part of the organ; each is connected with a large artery. Two longitudinal furrows, one anterior, the other posterior and less defined, correspond with the position of the median partition which separates the two ventricles within. The right ventricle occupies more of the anterior, and the left ventricle more of the posterior, surface of the heart; the left ventricle reaches lower than the right, and so forms alone the apex of the heart, the longitudinal furrows and septum terminating a little to the right of the apex. Each of the four cardiac cavities requires further description.

The *right auricle* (fig. 105, 3) consists of a larger part, named the *sinus*, and a smaller part leading from it in front, named the *appendix auriculæ* or *proper auricle*, so called on account of its resemblance to a dog's ear. The margins of the appendix are notched, and its walls, instead of being thin and smooth, like those of the sinus, are thick, and marked internally by prominent fleshy bands, the *musculi pectinati*. Into this auricle the systemic veins open, viz., the *superior vena cava*, 1, at the upper and forepart of the sinus; the *inferior vena cava*, 2, at its lowest part; and, lastly, the large *coronary vein* at the back, its orifice being protected by a thin membranous valve, the *coronary valve*, or *valve of Thebesius*; besides this, there are numerous apertures of small veins belonging to the heart, and certain recesses in the auricular walls. Upon the septum, between this and the left auricle, is an oval depression, the *fossa ovalis*, bounded above, and at the sides, by a margin named the *annulus ovalis*. The fossa ovalis is the vestige of an opening, the *foramen ovale*, which exists before birth, then permitting the blood to pass from the right into the left auricle: sometimes the foramen ovale is not entirely obliterated, in that case, a small valved aperture leading obliquely, beneath the annulus ovalis, into the left auricle. Attached to the anterior margin of the orifice of the inferior vena cava, is a thin membranous semi-lunar fold, called the *Eustachian valve* (fig. 105), the free concave border of which is turned upwards and to the left; it is often small, frequently perforated, and sometimes wanting. Before birth, it is large, and of great importance in directing the course of the blood.

Lastly, in front and to the left of the opening of the inferior cava, is the large aperture leading into the right ventricle, named the *right auriculo-ventricular* opening.

The *right ventricle*, 4, forms a somewhat conical cavity,

Fig. 105.

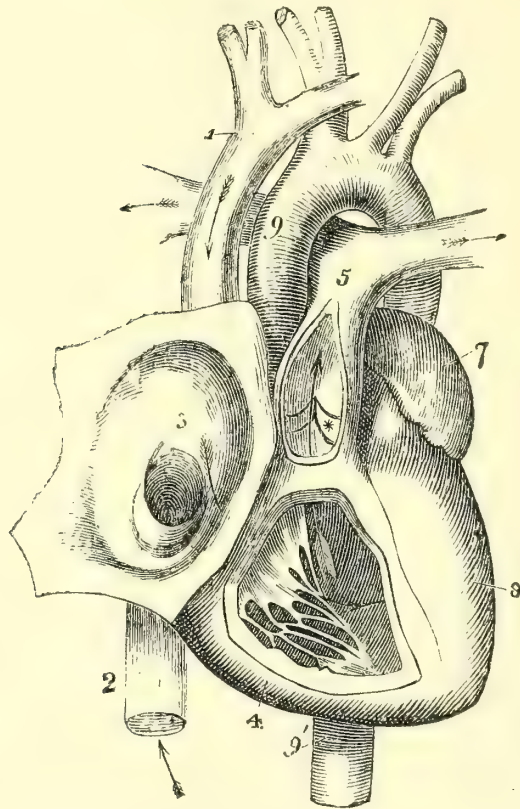


Fig. 105. Diagram of the heart and great bloodvessels. The right cavities of the heart, or right auricle and ventricle, and the pulmonary artery, are supposed to be laid open. 1, the superior vena cava; 2, inferior vena cava; 3, right auricle laid open, showing the orifice of the superior and inferior cavæ, the latter guarded by the Eustachian valve; 4, right ventricle laid open, showing the anterior segment of the tricuspid valve, its chordæ tendineæ, and muscoli papillares. The thin walls of the auricle, and the thicker walls of the ventricle, are seen on their sections; 5, pulmonary artery laid open, to show parts of two of its semilunar valves*; 7, part of the left auricle: the pulmonary veins are not represented, being concealed at the back of the heart; 8, the left ventricle; 9, the aorta, giving off branches to the head and upper limbs, and arching down to form the abdominal artery, which supplies branches to the rest of the body. The arrows show the course of the blood from the veins, 1, 2, to the right auricle; 3, through the auriculo-ventricular opening into the right ventricle, 4, and thence along the pulmonary artery, 5.

shut off from the left ventricle by the thick interventricular septum. At its base, is the opening from the auricle just mentioned, whilst above, and in front of this, is the aperture leading into the *pulmonary artery*. That portion of the ven-

tricle conducting to the artery, forms a conical prolongation, named the *infundibulum* or *conus arteriosus*. Both of these openings are guarded by remarkable valves. The auriculo-ventricular opening corresponds with the middle of the sternum, on a level with the third intercostal spaces and fourth costal cartilages. It is somewhat oval, and measures about $1\frac{1}{2}$ inch in diameter, in the male. It is surrounded by a strong fibrous ring, and its valve, being composed of three pointed segments, is hence called the *tricuspid valve*. These segments, of a trapezoidal shape, are formed by a doubling of the lining membrane of the heart, enclosing bands of fibrous tissue, and, it is said, a few muscular fibres; the segments are continuous at their base, and are there fixed to the fibrous ring around the opening into the auricle (fig. 106 *a*, 2). Of the three segments, one corresponds to the front of the ventricle, another to its posterior wall, and the third, the largest, lies between the auriculo-ventricular opening and the pulmonary artery. Each segment is thicker at its centre; whilst its margins are thinner, more transparent, and indented. To the margins, and also to the ventricular surfaces of the segments, are attached numerous fine tendinous cords, the *chordæ tendineæ* (fig. 105), the other ends of which are connected either with certain muscular *columns*, to be presently described, projecting from the walls of the ventricle, or with the inner surface of that cavity, especially with the septum. The *chordæ tendineæ*, proceeding from the adjacent margins of any two segments of the valve, are connected with the same muscular column. Some of the cords are inserted into the base of the segments, others are connected with its central thicker part, whilst the finest and most numerous are inserted into its thin marginal portion.

The muscular bands just mentioned, named the *columnæ carneæ*, are found in nearly every part of the inner surface of the ventricle. They are of three kinds: first, some which form merely irregular, and frequently reticulated, prominences on the sides of the cavity; a second kind are adherent at each end, though free in the middle; lastly, a third kind, considerably larger than the others, and named the *musculi papillares*, form three or four bundles, which project upwards from the walls of the ventricle, and are connected with some of the *chordæ tendineæ* of the tricuspid valve. The internal surface of the infundibulum is smooth.

The orifice of the pulmonary artery, fig. 105, 5; corresponds with the upper border of the third left costal cartilage, and

second intercostal space, close to the sternum. It is circular, and measures, in the male, a full inch in diameter. Its protecting valves consist of three semi-circular membranous folds, named *semi-lunar valves* (fig. 105*, fig. 106, 4), attached, by their convex margins, to the sides of the pulmonary artery at its line of junction with the ventricle, but free at their straight borders, which are turned upwards in the direction of the artery. In the middle of the free border of each valve, is

Fig. 106.

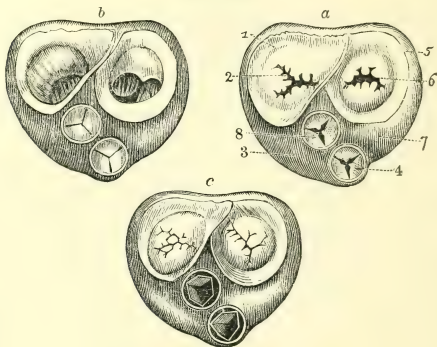


Fig. 106. Three views of the base of the heart, after removal of the auricles; the commencements of the pulmonary artery and the aorta are left, in order to show the valves of the heart and their altered positions at different moments of the heart's action. *a*, 1, interior of part of the right auricle; 2, right auriculo-ventricular, or tricuspid valve; 3, right ventricle; 4, pulmonary artery and its semilunar valves; 5, interior of part of the left auricle; 6, left auriculo-ventricular, bicuspid, or mitral valve; 7, left ventricle; 8, aorta, and its semilunar valves. In this view, all the valves have their segments a little apart. *b*, shows the auriculo-ventricular apertures open, and their valves apart; the arterial orifices are closed, and their valves in contact: condition during diastole of the ventricles. *c*, shows the opposite conditions of the valves; condition during systole of the ventricles.

a small fibro-cartilaginous nodule, the *corpus Arantii*. When stretched across the vessel, the borders meet each other, forming lines diverging from the centre at angles of 120° . The free and attached margins of each valve contain tendinous fibres; tendinous fibres also radiate across the valve, from the corpus Arantii to its attached margins, so that two thin semi-

lunar portions, called *lunulae*, are left, one on either side of the nodule. Behind the segments, the pulmonary artery presents, at its base, three slight dilatations or pouches, the *sinuses of Valsalva*.

The *left auricle* (fig. 105, 7), somewhat smaller than the right, has thicker walls, measuring, on an average, $1\frac{1}{2}$ line in thickness, whilst those of the right auricle measure only 1 line. Like the latter, it consists of a *sinus* and an *appendix*. The sinus is placed behind the aorta and pulmonary artery. The appendix, projecting forwards and to the left side, is narrower, and more curved and notched, than the right one; its *musculi pectinati* are smaller and less numerous. At the back of the auricle are the openings of the four *pulmonary veins*, two on each side, their orifices being destitute of valves. On the septum, between this and the right auricle, is a lunated depression, bounded below by a crescentic ridge, the vestige of the foramen ovale. At the lower part of the auricle, is the opening into the left ventricle, or left *auriculo-ventricular* opening.

The *left ventricle*, 8, is longer, and more conical in shape, than the right ventricle; it has much thicker walls, the proportion being as 3 to 1. The walls are thickest opposite the middle of the cavity, and thinnest at the apex, whilst the right ventricle is thickest near its base. The average thickness, in lines, of the walls of the two ventricles in the male, in whom they are somewhat thicker than in the female, are, for the left ventricle, at the base, middle, and apex, $4\frac{1}{2}$, $5\frac{1}{6}$, and $3\frac{3}{4}$; and for the right, $1\frac{1}{6}$, $1\frac{3}{8}$, and $1\frac{1}{30}$. (Bizot). The left ventricle increases in thickness as life advances; but the right remains unaltered after the period of full development.

At the left and hinder part of the base of this ventricle, is the oval opening from the left auricle; in front and to the right of this, is the circular aperture of the *aorta*. These openings are, after death, smaller than the corresponding orifices on the right side of the heart. The annexed Table shows the circumference of all four apertures, in the adult male and female (Peacock):—

		MALE.		FEMALE.	
		Inches	Lines	Inches	Lines
Auriculo-ventricular openings	{ right	4	6	4	0
	{ left	3	7	3	10
Arterial openings	{ pulmonary	3	4	3	3
	{ aortic	3	0	2	10
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The left auriculo-ventricular opening corresponds to the centre of the sternum, reaching upwards a little to the left. It is guarded by a valve, resembling the tricuspid valve, but formed of two segments instead of three, and hence called the *bicuspid* or *mitral valve* (fig. 106, 6). The two segments are named, from their relative position, anterior and posterior; the former is somewhat the larger. The segments are provided with *chordæ tendineæ*, fewer in number than those of the tricuspid valve, but having similar attachments; all these structures are stronger and thicker than those of the right ventricle. The internal surface of the left ventricle generally, like that of the right, is provided with three kinds of *columnæ carneæ*, which, however, are relatively small and numerous; there are only two *musculi papillares*.

The round orifice of the aorta lies behind the junction of the third left costal cartilage with the sternum. It is separated from the auriculo-ventricular opening, by the base of the anterior segment of the bicuspid valve, here joined to the aortic fibrous ring. The aortic orifice is protected by three *semilunar valves* (fig. 106, 8, fig. 107, *b*, 2), resembling those of the right side in form, in their mode of attachment to the sides of the great bloodvessel, and in the peculiar direction of their free edges towards the artery; but they are thicker and stronger, have their *corpora Arantii* larger, and their lunular margins more developed. The pouches, or *sinuses of Valsalva*, at the base of the aorta, are also larger than those of the pulmonary arteries. The two coronary arteries, or nutrient arteries of the heart, arise from the bottom of two of these pouches, close behind the corresponding semilunar valves.

The cavities of the heart are lined by a very fine serous membrane, named the *endocardium*, which is continuous with the lining membrane of the large vessels; it is somewhat thicker in the auricles than in the ventricles, and thicker in the left than in the right cavities; the valves of the heart consist essentially of folds of this membrane, enclosing fibrous tissue. It is difficult to determine the capacity of the cavities of a muscular organ like the heart; the estimates given of the capacity of the left ventricle, vary from 4 to 6·3 oz.; the right ventricular cavity is usually said to be a little larger. The capacity of each auricle corresponds with, or is a little smaller than, that of the respective ventricle.

The muscular fibres of the heart.—The substance of the heart is almost entirely composed of *muscular fibres*, arranged

Fig. 107.

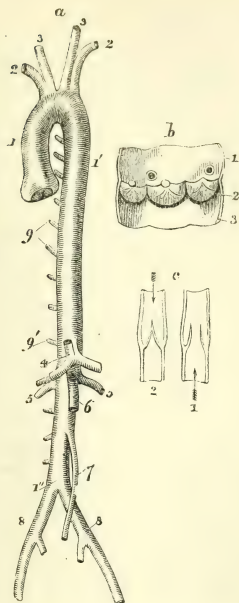


Fig. 107. *a*, the aorta detached from the heart and from the body. 1, ascending aorta, showing the enlargements or pouches at its commencement, known as the sinuses of Valsalva; 1', 1'', descending aorta, thoracic and abdominal; 2, 3, 3, 2, branches from the arch of the aorta, which supply the head and upper limbs; 4, coeliac axis, or artery, which divides into three branches to supply the stomach, liver, and spleen; 5, renal arteries for the kidneys; 6, superior, and 7, inferior mesenteric arteries which supply the small and large intestine; 8, 8, iliac arteries, which give off branches to the pelvis and lower limbs; 9, 9', intercostal and lumbar arteries, which supply the walls of the thorax and abdomen. *b*, portion of the left ventricle, and the commencement of the aorta, laid open, to show the aortic semilunar valves; 1, portion of the aorta, with the orifices of the coronary arteries, or nutrient arteries, of the heart; 2, the three valve segments; 3, portion of the left ventricle. *c*, diagrams, to show the action of the valves in the veins; 1, the valves open, so that the blood can pass on; 2, valves closed, so that the backward flow of the blood is arrested.

in layers, covered externally by a reflection of the serous membrane of the pericardium, and lined, within the cavities, by the endocardium. Four fibrous rings also exist, viz. those around the two auriculo-ventricular openings and the orifices of the pulmonary artery and aorta. Besides this, the heart possesses proper arteries, capillaries, and veins, deep and superficial lymphatic vessels, and numerous nerves and nervous ganglia.

The fibrous rings of the left side of the heart, are, like the valves, stronger than those of the right side. Those of the auriculo-ventricular orifices give attachment to the segments of their respective valves, and also to a few of the muscular fibres of the auricles and ventricles. The rings surrounding the orifices of the pulmonary artery and aorta, present a smooth ventricular border, attached to the muscular substance of the ventricles; and a deeply-notched arterial border, with which the pouches of Valsalva are connected. When the heart of an animal is boiled, so as to harden its muscular, and to gelatinise its fibrous, portions, the auricles and great blood-vessels may be easily separated from the ventricles; three apertures only are then seen in the muscular substance of the base of the ventricles; viz. one for the left auriculo-ventricular opening, another for the orifice of the pulmonary artery, and a third, the largest, common to the left auriculo-ventricular opening and the aortic orifice; for the fibrous rings around these two latter are conjoined at one point. Behind the aortic orifice, and between the two auriculo-ventricular openings, is a piece of fibro-cartilage, which, when ossified, forms the *bone of the heart*.

The heart, though an involuntary muscle, has dark red fibres, marked with transverse striæ, like those of the voluntary muscles; but they differ, in being often branched and joined together again, and in having their fasciculi interlaced; moreover, the fibres are somewhat smaller, less distinctly striated, sometimes marked by faint longitudinal streaks, and, for the most part, are not attached to tendinous structures: the sarcolemma of each fibre is not easily seen, excepting in fatty degeneration of the fibres. There is scarcely any areolar tissue between the fibres, hence the characteristic firmness of the contracted heart.

The arrangement of the muscular fibres of the heart, is one of the most difficult subjects of investigation. Vesalius, Albinus, and even Haller, were unable to follow them; and

very different and complicated descriptions of the fibres have been given by Lower, Winslow, Senac, Wolff, Gerdy, Duncan, Reid, Budge, and, more recently, by Pettigrew.

After long boiling or maceration in pure alcohol, the fibres of the auricles, but especially those of the ventricles, may be stripped off, and unwound in flat bands or *layers*. The auricular and ventricular fibres are quite independent, the auriculo-ventricular fibrous rings, with the pericardium and endocardium, forming the sole bond of union between them.

The fibres of the *auricles*, consist of a superficial and deep layer. The *superficial* layer is thin, incomplete, and common to both auricles; its fibres are transverse, and chiefly found on the front of the auricles; a few enter the septum. The *deep* layer consists of looped and annular fibres proper to each auricle; the *looped* fibres are fixed, by both ends, to the corresponding fibrous ring, and pass, in various directions, over the surface of the auricle; the *annular* fibres embrace the auricular appendages, and also surround the large venous openings in each auricle, extending both over the auricle and the veins.

The fibres of the *ventricles*, first studied by Lower (1669), present a far more complex arrangement. They present numerous, and somewhat easily separable, layers, having a general spiral arrangement around those cavities. The superficial fibres pass, more or less obliquely, downwards from right to left, on the front of the ventricles, and, in the opposite direction, i.e. upwards from right to left, at the back of the ventricles. A few of these fibres are almost vertical. On the posterior or under surface of the heart, many of the superficial fibres are common to both ventricles, passing from one to the other, over the line of the septum, the surface being flattened, and the two ventricles blended together. On the upper surface, or in front, however, a great number of the superficial fibres dip in at the line of the septum, decussating with each other, so that the ventricles are here more distinct; nevertheless, some of these fibres pass from one ventricle to the other. When these are removed, the deeper fibres are found to be chiefly proper to each ventricle; so that, as said by Winslow, the ventricular portion of the heart seems to be composed of two hearts, enveloped in a third. As the fibres become deeper, they are less and less oblique, until, at last, they are nearly transverse, excepting such as ascend on the inside of the ventricles. According to their mode of dissection, different

anatomists make different numbers of layers, and some divide these into numerous component bands. According to Pettigrew, the latest authority, there are *seven* layers, three outer ones, the fibres of which become successively less and less *oblique* downwards from right to left, a central *transverse* layer, and three inner ones, the fibres of which become more and more *oblique* in the opposite direction.

The ventricular fibres, whether superficial or deep, have long been known to form spirals, at and near the apex of the heart, the superficial fibres forming a completely closed spiral, and each succeeding layer a more open one. Hence, on looking directly at the apex of the heart, a remarkable whorl, or vortex, of fibres is seen, in which these appear, in turn, to sink towards the interior of the ventricles; if the fibres of each layer be now raised up and removed, the vortex becomes more and more open, and at length the cavities of the ventricles are exposed.

It was believed by Lower, Gerdy, Reid, and other anatomists, that the ventricular fibres chiefly, if not entirely, arise from the auriculo-ventricular fibrous rings, and that, after passing spirally round the heart, they turn upon themselves at the apex, there forming, as indicated especially by Lower and Gerdy, twisted continuous loops, and then pass up directly through the walls or septum of the ventricles, back to the fibrous rings again, or reach them indirectly, through the muscoli papillares and chordæ tendineæ of the tricuspid and bicuspid valves. In short, the fibres of the ventricles were described as forming loops, open towards the base of the heart, but closed, and twisted into a vortex, at the apex. However, according to Duncan, the fibres form loops in the direction of the base, as well as in that of the apex; and Pettigrew affirms that none, or almost none, are attached to the fibrous rings, but pass by them, in the form of loops. Moreover, the elaborate dissections of the last-named anatomist, show, that just as, at the apex, the superficial fibres penetrate, to become, as has been long known, the deep-seated fibres, so, at the base, the superficial fibres are likewise continuous with the deepest fibres.

In the left ventricle, which Pettigrew regards as the typical ventricle, the first, or superficial layer, passes, both at the apex and base, into the innermost or seventh layer, the second into the sixth, and the third into the fifth; the fourth layer is central, and forms a transverse layer situated between the third and the fifth. Each successive double layer encloses the

next in order, and the necessary limitation of the central layer, and its absence at the apex and base, account for the greater thickness of the walls of the left ventricle, across its middle. The spiral fibres, which may be traced from the front of the auriculo-ventricular opening, pass over the anterior surface of the ventricle, and, after describing one turn and a half, dip into the apex posteriorly; whilst those coming from the back of that opening, pass over the hinder surface of the ventricle, wind forward, and enter the apex anteriorly; after dipping inwards, the former end in the anterior muscoli papillares and columnæ carneæ, and the latter, in the posterior muscoli papillares and columnæ carneæ. The spiral and interwoven arrangement of all these layers, must assist the powerful and simultaneous contraction of the ventricular walls, and may perhaps explain the rotatory movement of the heart during each beat, to be hereafter noticed.

The structure of the right ventricle is similar, but less complete. Internal to the fourth layer, the fibres of the one ventricle are altogether independent of those of the other. The layers of the right ventricle, are continued into each other, not at the apex only, as in the case of the left ventricle, but also along the whole length of the septum. The right ventricle is regarded, by Pettigrew, as a sort of segment of the left one, and he refers to the shape and perfection of structure of the latter, and also to the position, and the mode of development, of the septum, from a protrusion of the anterior wall of the single ventricle of the primitive heart, as according with this view.

The ventricular fibres, in the hearts of the Mammalia generally, seem to be arranged on the same plan as that of the human heart; and a correspondence is observed in the disposition of these fibres in the Bird, Reptile, and Fish.

The nutrient arteries of the heart, are the two *coronary arteries*, the first branches given off from the aorta; they arise just beyond the semilunar valves, wind round the auriculo-ventricular groove, and give off two chief branches which run along the furrows between the ventricles. The *cardiac veins* end chiefly in a short trunk, named the *cardiac sinus*, which opens into the back of the right auricle, and is protected by the valve of Thebesius, already described; this sinus is interesting, as being the persistent portion of the lower end of the left descending vena cava of the early embryo, the remainder of which closes from the root of the neck down to this

sinus, leaving only certain vestiges behind. Numerous small cardiac veins enter the right auricle by separate openings. It has been supposed by some, that the blood may pass directly from the cavities into interstices in the tissue of the heart, and this appears to be the case in the heart of the frog and of certain Fishes, in which only one ventricle exists, containing a uniform fluid: but this could hardly occur in the hearts of the warm-blooded Birds and Mammalia, in which there are two separate ventricles, one containing dark or impure blood. In these, ample provision exists, in proper arteries, capillaries, and veins, for a special nutrient circulation. The *lymphatics* are superficial (fig. 101) and deep. The *nerves* of the heart are derived, on each side, from the pneumogastric nerves, and from the sympathetic system. The former give off cardiac branches from their trunks, and also from their recurrent laryngeal branches; whilst the latter give off sympathetic cardiac branches from the cervical ganglia. The phrenic nerves send offsets to the pericardium, and possibly a few fibres to the heart itself. The sympathetic and pneumogastric branches unite to form the *cardiac plexuses*, from which small plexuses and branches proceed along the coronary arteries. Certain important ganglia exist upon the heart; the *ganglion of Wisberg* lies beneath the arch of the aorta, and in animals, as in the calf and frog (Remak), others are found about the base of the ventricles. In the course of the cardiac nerves, certain enlargements have been described as microscopic ganglia (Lee); but, according to other anatomists, these are thickenings of the sheaths of the nerves. The lining membrane of the sinus of the right ventricle, is most abundantly supplied with nerves.

Course and Causes of the Circulation.

In moving through the human body, the blood takes the following definite *twofold* course, the circulation in Man, like the heart itself, being *double*. Proceeding from the left side of the heart through the aorta (fig. 108, 9, 9), and its various branches called the *systemic arteries*, the blood is distributed to every part of the frame, reaching the *capillary vessels* throughout the body generally; from these capillaries, it passes into the minute venules, and, collected into larger and larger *veins*, 1, 2, finds its way back to the right side of the heart, 3, 4: this part of the circulation is called the *greater* or *systemic* circula-

tion. From the right side of the heart, 3, 4, the blood issues through the *pulmonary artery*, 5, and by its branches is conveyed to the lungs, passes through the *pulmonary capillaries*, is collected by the *pulmonary veins*, 6, and so returns once more to the left side of the heart, 7, 8 : this part of the circulation, is called the *lesser* or *pulmonary circulation*. In the systemic circulation, therefore, the blood leaves the left side of the heart, and returns to the right side ; in the pulmonary circulation, the blood leaves the right side and returns to the left. The left side of this organ, is sometimes called the systemic, and the right side the pulmonary, heart. The greater circulation being performed through the body generally, and the lesser circulation through the lungs, the two are continuous, at the heart, with each other, a given portion of blood passing first through the one, then through the other, afterwards through the former again, and so on. The *portal* circulation, already described (p. 68), is a special offset of the systemic circulation.

The history of the discovery of the Circulation, affords a good illustration of the slow and laboured steps, by which man arrives at true knowledge. By Hippocrates, 400 B.C., the veins and arteries were confounded under one name, *φλεβέες*, *phlebes*, the word, *artery*, being applied by him to the *trachea* or windpipe. Aristotle distinguished the arteries from the veins, and noticed that the former were usually found empty of blood, containing only air : the heart, however, was known by him to be in connection with the veins, and these were supposed to convey the blood *into* the body. Galen was the first to maintain that the arteries contained blood as well as air. Vesalius pointed out that the two sides of the heart have no direct communication. Servetus demonstrated the passage of the blood through the lungs. The term 'circulation' first occurs in the writings of Cæsalpinus, who had access to a treatise by Servetus. At length, in 1628, William Harvey published, in his work, '*De motu cordis et sanguinis*'—on the motion of the heart and blood—an account of his great discovery, or demonstration of the real course of the blood, or of the Circulation. He founded his conclusions, first, on the anatomical connections and continuity of the heart, arteries, and veins ; secondly, on the facts, that on dividing an artery, blood issues from that end which is still connected with the heart, whilst on dividing a vein, the blood comes from the end furthest from the heart ; thirdly, on the fact that a vein, when tied, swells on the side of the liga-

ture furthest from the heart; and lastly, on the direction of the valves in the veins, and of those situated in the heart itself. Afterwards, the mode in which the blood passes from the

Fig. 108.



Fig. 108. Diagram of the cavities on the two sides of the heart, to show the course of the blood through it. 1, Vena cava superior; 2, vena cava inferior; 3, right auricle; 4, right ventricle; 5, pulmonary artery; 6, 6, pulmonary veins, right and left; 7, left auricle; 8, left ventricle; 9, aorta; 10, hepatic veins. The dark parts are those which contain venous blood; the light parts contain arterial blood. The arrows indicate the course of the blood within the heart, and through the lungs and the body. Thus, the dark blood returns from the upper half of the body by the superior vena cava, 1, and from the lower half of the body by the inferior vena cava, 2, joined by the hepatic veins, 10; it enters the right auricle, 3, passes into the right ventricle, 4, and then through the pulmonary artery, 5, and it branches through the capillaries of both lungs. Here, it is changed into red blood; gathered then into the pulmonary veins, 6, 6, it enters the left auricle, 7, passes into the left ventricle, 8, and thence through the aorta, 9, and its branches, into the capillaries of all parts of the body. Here it again becomes dark, and is once more returned by the venæ cavæ, 1, 2, to the right side of the heart. It is seen that the right and left sides of the heart do not communicate. The one always contains dark, the other red blood.

arteries into the veins, not quite understood by Harvey, was explained by Malpighi's discovery of the capillary vessels, in the frog's foot, in 1661.

The *proofs* of the circulation of the blood, now usually advanced, are identical with those just mentioned, viz. the anatomical connection and continuity of the heart, arteries, capillaries, and veins; the different direction in which the blood escapes from a cut artery and a cut vein; the effect of ligature upon the veins; the special direction of the valves of the heart and veins; and lastly, the actual observation of the blood moving in the capillary vessels of the transparent parts of animals, such as the translucent bodies of the larvæ, or young, of Amphibia and Fishes, the gills of the tadpole, the web of the frog's foot, the mesentery of the mouse, the wing of the bat, and even the retinae of our own eyes.

The chief *cause* of the motion of the blood, is the contraction of the muscular walls of the heart upon its fluid contents. But the movement of the blood, is modified by the elasticity and muscular contractility of the coats of the arteries; it is aided by the pressure of the muscles of the body upon the veins, and likewise, to a certain degree, by the movements of the walls of the chest in respiration. Perhaps also the changes incidental to nutrition, secretion, excretion, and respiration, which occur in the blood, in the systemic and pulmonary capillaries, may influence its motion through them. The *direction* of the blood-current, is primarily determined by the valves within the heart, and is aided by those within the veins.

Action of the Heart.

The heart, the great agent concerned in the circulation, propels the blood from its interior, into the body and lungs, by means of successive contractions of its ventricular walls. The contractility of its muscular tissue, is the immediate source of the motor power which impels the blood through the body. The suspension of the heart within the smooth pericardium, facilitates its movements; whilst the equally smooth endocardium diminishes the friction of the blood against the walls of its cavities. The heart has been likened to a force-pump, but this is a rude comparison; for a pump is a passive apparatus, through which some extrinsic force operates; whereas the heart, alternately dilating and contracting, first receives the blood from the veins, and then drives it into the arteries, by means of a force resident in its own walls. In this action, the right and left auricles dilate and contract together; and the right and left ventricles also dilate and contract together.

The contraction of the two ventricles, always takes place immediately after that of the two auricles; and when the ventricles have contracted, an interval, or *pause*, occurs, before another contraction of the auricles takes place, and during this pause, both sets of cavities are gradually *dilating*. The contraction of the auricles and ventricles, is named their *systole*, whilst their dilatation is called their *diastole*; the order of the successive dilatation and contraction of these parts, was compared by Harvey to the successive movements of deglutition. Thus, when the auricles are dilating, they receive blood from their respective veins, and when they contract, they force the blood into the ventricles, which are then dilating to receive it; when the ventricles are filled, they in turn contract, and propel the blood into the great arteries. But the right auricle receives the blood from the body generally, and the right ventricle propels it into the lungs; whilst, of the left cavities of the heart, parted off completely from the corresponding cavities of the right side, the left auricle receives the blood from the lungs, and the left ventricle propels it into the body. As the auricles merely propel the blood into the ventricles, their walls are comparatively thin, whilst the thicker walled ventricles have relation to the greater work they have to perform. The proportionately greater thickness of the walls of the left ventricle, and the greater strength of the mitral and aortic semilunar valves, as compared with the tricuspid and pulmonary semilunar valves on the right side of the heart, have reference to the greater force needed to distribute the blood through the body, than through the lungs.

On tracing the course of the blood, through the body and the four cavities of the heart, it is found that, proceeding from the left ventricle (fig. 108, 8), the blood passes, through the aorta and arterial system, into the capillaries of the whole body, and thence back by the systemic veins, 1, 2, into the right auricle, 3; from the right auricle it passes into the right ventricle, 4, and thence proceeds through the pulmonary arteries, 5, capillaries, and veins, 6, 6, of the lungs, into the left auricle, 7, from which it passes into the left ventricle, 8, and thence is propelled, as before, through the aorta, 9, into the arteries of the body.

The mechanism and details of these movements, are very complex. As the auricles dilate, the blood enters and distends them, that filling the right auricle, coming from the two *venæ cavæ* and the nutrient veins of the heart itself, that filling

the left auricle, from the four pulmonary veins. As the auricles are filling, some of the blood passes through them, into the corresponding ventricles, but the instant the auricles are fully distended, they contract, and discharge nearly the whole of their contents into the ventricles, which, at this period, are dilating to receive the blood. The backward flow of the blood from the auricles into the veins, is checked, more or less completely, by the contraction of the muscular fibres surrounding the orifices of the *venæ cavæ* and pulmonary veins, and, as regards the right auricle, by the Eustachian and Thebesian valves, at the mouths of the inferior vena cava and cardiac sinus, and by those in the great veins at the root of the neck. The blood passes from the auricles into the ventricles, through the right and left auriculo-ventricular openings; the tricuspid and mitral valves, placed respectively at those openings, having the free borders of their segments directed towards the ventricles, offer no opposition to this movement of the blood; but the gradual filling of the ventricles, and especially their complete distension, are accompanied by a closure of the segments of the valves, the blood getting behind them, or between them and the walls of the distended ventricles. The ventricles now contract, and propel the blood into the great arterial trunks proceeding from them, i.e. the right ventricle into the pulmonary artery, and through the lungs, and the left ventricle into the aorta, and through the body. The reflux of the blood towards the respective auricles, is now prevented by the sudden closure of the tricuspid and mitral valves, the segments of which are, moreover, prevented from being forced back into the auricles, by the *chordæ tendineæ* respectively attached to them. The blood, driven from the ventricles into the pulmonary artery and the aorta, opens the segments of the semilunar valves situated at the commencement of each of those vessels, and displaces onwards the column of blood contained within them, which, however, is not quite stationary. Four effects ensue: first, a vibratory impulse to the blood columns in the pulmonary artery and aorta, and in their branches; secondly, an increased velocity of the blood column; thirdly, an increased pressure within the arteries; and, fourthly, owing to the resistance offered by the blood in front, a distension of the elastic walls of the arteries themselves. But the ventricles, having contracted, after a short pause begin to dilate again, and then the columns of blood in the two great arteries, reacted upon by the recoil of the

distended and elongated coats of those vessels, would flow back towards the ventricles, if the segments of the semilunar valves did not speedily open out across the mouths of those vessels. The blood first getting into the pouches, or sinuses, of Valsalva behind the valves, an action which is facilitated by the projecting corpora Arantii, then presses on the whole arterial surface of the segments, and so regurgitation into the ventricles is prevented. The force which thus acts upon the two columns of blood, to close the semilunar valves, is the resilience of the coats of the previously distended arteries; but it is itself derived from the heart's action, which has caused distension of the vessels. As the muscular walls of the ventricles relax, and their cavities dilate, the tricuspid and mitral valves reopen, and blood passing from the auricles, begins to fill them again. In the meantime, the auricles themselves have been dilating to the point of distension, and again, at that moment, the actions of the heart necessary to the circulation recommence, viz., the rapid contraction of the auricles, the complete distension of the ventricles, and the sudden contraction of these cavities.

A complete action of the heart, consists of a single systole and diastole of its auricles and ventricles. The period occupied in such an action, commences with the systole of the auricles, includes the systole of the ventricles, and terminates at the perfect diastole of the auricles, when these cavities are fully distended, and ready to perform their systole again. During this period of a complete cardiac act, the auricles contract quickly, whilst the ventricles contract a little more slowly; but the auricles dilate slowly, whilst the ventricles dilate more quickly. Hence, (see the Table at p. 212,) the systole and diastole of the two sets of cavities, occupy different parts of the entire period of a single cardiac action or beat.

The *diastole* of both the auricles and ventricles, has been supposed to depend on an active contraction of particular sets of their muscular fibres; but it is now generally regarded as a passive phenomenon of dilatation, dependent on the rest or relaxation of all their fibres.

The *systole* of the auricles, consists of a progressive contraction, which spreads from the orifices of the great veins towards the auriculo-ventricular openings, the auricular appendices acting last; the auricles, therefore, contract towards the base of the ventricles. The systole of the ventricles is not only somewhat slower, but is more uniform than that of the auricles,

being simultaneous through every part of their walls, the total result being likewise to draw them towards their base, i.e. towards the orifices of the great arterial trunks. By this action, the ventricular portion of the heart is shortened, rendered thicker from back to front, and more convex on its anterior surface; it is also widened a little posteriorly (Budge); at the same time, it becomes very firm and hard, like any other contracted muscular mass. Owing to the elongation of the great arterial trunks, at the moment of their distension by the blood, the base of the heart descends within the thorax; moreover, the apex is tilted upwards, and lifted a little towards the left; whilst the entire heart, owing, perhaps, to the obliquity of its muscular bands, rotates slightly on its axis, and undergoes a screw-like motion to the right. The base of the heart appears to move to a greater extent than the apex, because the downward movement of the entire heart lessens the change of position upwards, caused by the contraction of the ventricles. Some even maintain that the apex is moved a little downwards and to the left.

These changes in the form and position of the heart, bring its anterior surface, a little above the apex, up to the walls of the chest, the pericardium, however, intervening, and produce a slight concussion against them. This, well known as the *impulse* of the heart, is felt most distinctly opposite a point a little below the middle of the ventricles, between the fifth and sixth ribs of the left side, 2 inches from the sternum. The impulse coincides with the systole of the ventricles.

The auriculo-ventricular valves, and the semilunar valves, are open and shut alternately at different moments of the heart's action; for the auriculo-ventricular valves are open, and the semilunar valves closed, during the diastole of the ventricles; whilst the former are shut, and the latter open, during the systole of those cavities. Their joint action is remarkable, for they determine, like the valves of a force-pump, the direction of the blood through the two sides of the heart, and hence the course of the circulation generally. The segments of the auriculo-ventricular valves, connected by the chordæ tendineæ with the sides, or with the muscoli papillares, of the corresponding ventricles, are first opened by the torrent of blood rushing from the auricle into the ventricle; then they are gradually raised from the sides of the ventricle, and suddenly closed, as is now generally maintained, by the action of the blood itself, during the ventricular diastole; although

Haller, from observations on a living animal, believed that their closure was in part due to the action of the papillary muscles. Immediately the ventricles begin to contract, so as to change the form and size of the cavities and auriculo-ventricular orifices, and press forcibly upon the contained blood, the valve-segments, as already stated, are prevented from being driven back into the auricle, by the chordæ tendineæ, which are kept *tense* by the muscoli papillares contracting simultaneously with the walls of the ventricles. Were it not for the existence of the papillary muscles, the chordæ tendineæ would be relaxed, and the segments of the valves would be more or less forced into the auricular cavities. The tricuspid valve is said to close less perfectly than the mitral (Hunter); thus a certain quantity of blood is driven back into the right auricle, and also beyond it, upon the blood in the great veins, producing a slight regurgitant flow, as far as the valves of the jugular veins, and causing a *venous pulse*, synchronous with the pulse in the *carotid arteries*. The reflux thus permitted from the right ventricle, is probably important, preventing the over-distension of that cavity by any temporary obstruction to the circulation through the lungs, from muscular effort, or cold; it has been found experimentally, that when the heart is forcibly distended, its pulsations are immediately arrested, a condition which is thus guarded against. It is certain that the quantity of blood delivered by the right auricle into the right ventricle, is subject to variation; whilst that propelled from the left auricle into the left ventricle, is probably uniform; on that side of the heart, the mitral valves close accurately, and no regurgitation takes place. Vierordt, however, doubts the normal occurrence of any reflux, even on the right side, because no such regurgitation takes place during the auricular systole, nor yet any backward pressure in the venous trunks.

The semilunar valves at the orifices of the pulmonary artery and aorta, have no chordæ tendineæ, but they meet accurately across the orifices of those vessels, the little corpora Arantii assisting in the complete closure of the three segments in the centre. These valves, opened by the blood projected from the ventricles, would be closely applied to the walls of the arteries, were it not for the presence of the pouches of Valsalva behind them; but the blood retained in those pouches, facilitates the separation of the valves from the sides of the vessels, and their subsequent opening out across those vessels, by the pressure of

the blood acted upon by the distended and resilient arteries. The shock of the columns of blood in the arteries, is sustained mainly by the stronger and more tendinous part of the valves, their thinner marginal lunules, being applied against each other, so as to form three lines radiating from the centre of the vessel between the contiguous borders of the valves. The greater the resilient force of the arteries, the more accurate and close is the apposition of the valves.

The closure of the auriculo-ventricular and the semi-lunar valves, is necessarily accompanied by a tightening out of their respective segments; this is the chief cause of certain sounds, which, on listening over the region of the heart, are heard, at stated intervals, in the period of each single cardiac beat. These *sounds of the heart* are *two* in number, in each beat. They are audible to the ear placed on the thorax; but they are commonly examined by the tubular instrument, named the *stethoscope*. In certain circumstances, they may be heard by the individual himself. The two sounds occur in quick succession, after which there is a period of silence, often named the *pause*. The *first sound* is deep, dull, and long; the *second* is higher in tone, sharp, and short. The first closely precedes the pulse at the wrist, and coincides nearly with the impulse of the heart; the second follows immediately after the pulse. Supposing the entire period of the heart's beat, to be divided into eight equal parts, the first sound and the brief period which elapses between it and the second, have been said to occupy four parts; the second sound, to take rather less than two; and the silent interval, or pause, between it and the recurrence of the first sound of the next beat, to occupy rather more than two parts (Laennec); hence the period of the sounds would be to the period of silence, as 3 to 1. But the proportions have been perhaps more correctly, stated to be 2 to 1 (Williams), or nearly 1 to 1. (Volckmann.)

From observations on living animals, it has been found that the first sound coincides with the systole of the ventricles, the closure of the auriculo-ventricular valves, the opening of the semilunar valves, and the entrance of the blood into the great arteries. At this period, the auricles are beginning to dilate. Moreover, the first sound is speedily followed by the pulse, that in the facial artery occurring about $\frac{1}{30}$ th of a second, and that in the radial artery at the wrist $\frac{1}{6}$ th of a second, afterwards. The *second* sound coincides with the closure of the semilunar valves, and the opening of the auriculo-ventricular

valves; whilst, at this period, the ventricles begin to dilate, and the auricles continue their already commenced diastole. The pause of silence, which succeeds to the second sound, coincides with the full dilatation, and the subsequent contraction, of the auricle, and also with the completed dilatation of the ventricles; during this pause, the semilunar valves are closed, and the auriculo-ventricular valves are open.

The *causes* of the heart's sounds, have been very closely investigated, owing to the changes which they undergo in disease, and to the peculiarity of the sounds which are then developed. The *first* sound is usually referred to the closure of the auriculo-ventricular valves, either, directly and solely, as being dependent on the sudden tension of their segments, or, partially and indirectly, as due also to the muscular sound of the contracting ventricular walls, the sudden passage of the blood into the great arterial trunks, and the impulse of the heart itself against the side of the chest. Unless these valves were closed, the walls of the ventricles would not act so forcibly as they do; neither would the blood rush into the great arteries, nor would the impulse of the heart be so decided. Whilst, therefore, as is commonly believed, the tension and vibration of the tissue of the closed auriculo-ventricular valves may be really the chief cause of this sound, yet the three other accessory causes, viz. the muscular sound of the ventricles, the sound of the moving blood, and its friction against the orifices of the arteries, and, lastly, the impulse of the heart against the chest, may contribute to the production of the sound as actually heard. But the importance of these causes has probably been overrated. That the muscular sound is not essential, is shown by the fact, ascertained experimentally, that the sounds are not heard, if the great veins be compressed, so that no blood enters the heart, although its contractions may continue; the production of any sound by the internal movement of the blood, or its rushing through the arterial openings, is doubtful; and ordinary muscular contraction does not give rise to any loud or sudden sound. The cause of the *second* sound appears to be better determined; it is attributed almost entirely to the tension of the suddenly closed semilunar valves, across the orifices of the aorta and pulmonary artery. The tension of the membranous substance of the valves, is sufficient to cause a loud sound; but, by many authorities, the collision of the columns of blood in the great arteries, against themselves, and against the valves,

so as to produce that tension, is regarded as a conjoint cause of the actual sound heard in the heart. When, in living animals, one segment of each of these valves, is held back by a hooked needle, so that it cannot close, the second sound of the heart ceases. This sound has also been imitated in dead animals, by injecting fluid into the aorta, against the valves. The occurrence of changes in, and the occasional cessation of, the second sound, in cases of disease of the semi-lunar valves, also favour this explanation; so, likewise, does the fact that the second sound is so short, and occurs at the instant of the tightening out of these valves, and not during their subsequent and quiet closure. Lastly, there is no other simultaneous condition, or action, of any part of the heart which could produce a sound; the ventricles and auricles are, at this time, both quietly dilating, and the resilience of the great arterial trunks, forcing the blood back upon the semi-lunar valves, is the only mechanical action then capable of causing a sound.

The contraction of the auricles, which occurs in the latter part of the pause in the heart's beat, produces no audible sound, unless the heart be exposed, and the stethoscope be placed upon it.

It is usually held to be confirmatory of the preceding views, as to the causes of the two sounds of the heart, that the first sound is more distinctly heard opposite the fifth intercostal space of the left side, below the left nipple, i.e. over the region of the apex of the ventricles, where these approach nearest to the walls of the chest, to which they communicate the sound; whilst the second sound is heard most clearly in the third left intercostal space, close to the sternum, i.e. over the base of the ventricles, and the commencement of the great arteries, where these approach nearest to the thoracic walls.

The difference in the pitch and character of the two sounds, is partly explicable thus: the deep and dull tone of the first sound, may depend on the greater size and deeper position of the auriculo-ventricular valves, on their thicker attachments, and on the quantity of muscular substance which overlies them; the higher and sharper tone of the second sound, may be connected with the thinner structure and attachments, and with the less covered position of the semilunar valves.

The following Table shows the order and duration of the complicated actions of the different parts of the heart during each complete beat, and also their relations, in point of time,

Sounds and Movements of the Heart.

Sounds and Pause	Duration in eighths of a Heart's beat	Condition of Ventricles	Condition of Auricles	Condition of Valves		Impulse of Heart Pulse
				Auric.-Vent.	Semilunar.	
First sound:— Systolic, longer, du 1, and deep	$\left. \begin{array}{c} \cdot \\ \cdot \\ \cdot \end{array} \right\} \frac{4}{8}\text{ths.}$	Contracting . $\left. \begin{array}{c} \cdot \\ \cdot \\ \cdot \end{array} \right\} \text{Systole}$	Dilating . $\left. \begin{array}{c} \cdot \\ \cdot \\ \cdot \end{array} \right\} \text{Diastole}$	Closed .	Open .	$\left\{ \begin{array}{l} \text{Impulse. Pulse} \\ \text{at wrist, } \frac{1}{8}\text{th} \\ \text{of a second} \\ \text{later.} \end{array} \right\}$
Second sound:— Diastolic, shorter, sharp, and higher . . .	$\left. \begin{array}{c} \cdot \\ \cdot \\ \cdot \end{array} \right\} \begin{array}{l} \text{rather less than} \\ \frac{2}{8}\text{ths} \end{array}$	Dilating . $\left. \begin{array}{c} \cdot \\ \cdot \\ \cdot \end{array} \right\} \text{Diastole}$	$\left\{ \begin{array}{l} \text{Dilating or} \\ \text{Dilated .} \end{array} \right\}$ Dilated .	Open .	Closed	
	$\left. \begin{array}{c} \cdot \\ \cdot \\ \cdot \end{array} \right\} \frac{1}{8}$ rather more than $\frac{2}{8}\text{ths}$	Dilating . Dilated .	Contracting . $\left. \begin{array}{c} \cdot \\ \cdot \\ \cdot \end{array} \right\} \text{Systole}$	Open .	Closed	
Period of silence	$\left. \begin{array}{c} \cdot \\ \cdot \\ \cdot \end{array} \right\} \frac{1}{8}$		Contracting . $\left. \begin{array}{c} \cdot \\ \cdot \\ \cdot \end{array} \right\} \text{Systole}$	Closing .	Closed	

to the two sounds of the heart, to the subsequent pause or interval of silence, and to the occurrence of the pulse at the wrist. The duration of the events is given after Laennec.

It is seen that the first sound occupies $\frac{1}{2}$ of the entire beat, the second nearly $\frac{1}{4}$ of the beat, and the period of silence rather more than the remaining $\frac{1}{4}$. The Table likewise exhibits the alternation of the systole and diastole of the auricles and ventricles, as well as the relative duration of their respective systolic and diastolic conditions. Thus the rapid systole of the auricles, occupies only $\frac{1}{8}$ th of the whole period, and their diastole $\frac{7}{8}$ ths; whilst the slower systole of the ventricles occupies $\frac{1}{2}$, and their diastole the other $\frac{1}{2}$ of the whole period or beat. According to Vierordt, the period of diastole of the auricle, is really shorter, being only $\frac{2}{8}$ ths or $\frac{3}{8}$ ths of the whole period; the remaining $\frac{4}{8}$ ths or $\frac{5}{8}$ ths of that time, usually regarded as the period of diastole, must, in that case, be viewed as representing a distended, or continued dilated, condition of the auricle. In the Table, the systole of the auricles and ventricles together, is seen to occupy $\frac{5}{8}$ ths, and the interval between the contraction of the ventricles and the commencement of the next beat, $\frac{3}{8}$ ths of the whole period. According to Cheveau, however, the ventricular systole in the horse, occupies only a little more than $\frac{1}{2}$ th of the entire beat; Sanderson's researches coincide with this statement as to the great rapidity of that event.

At each beat of the heart, the ventricles are supposed to be almost completely, if not entirely, emptied; the left ventricle is often found in that state after death, especially if examined during the period of the rigor mortis. On a section, the walls of that ventricle are then seen to be so thick, from their contraction, as to have been frequently described as being hypertrophied. Although the right ventricle, as already mentioned, allows a little blood to escape back into its corresponding auricle, yet both ventricles are supposed to throw practically, equal quantities of blood; for, unless this were so, the left ventricle would receive either too little or too much blood from the synchronous action of the right ventricle, the quantity of water lost, as vapour, from the blood, in its course from one ventricle to the other, through the lungs, being insignificant, amounting to less than $\frac{1}{6}$ th of a grain, during each beat of the heart. The quantity of blood thrown at each systole, by the ventricles, was formerly said to be, in the adult, about 4 oz., which was described as the normal capacity of each of those cavities;

but the most recent researches have led to higher estimates, viz. 5·3 oz. (Valentin), 6·2 oz. (Volkmann), and even 6·3 oz. (Vierordt.) Positive measurements are impossible; the results obtained, rest on various calculations in hæmadynamics, to be hereafter mentioned. The capacity of the auricles is said to be rather less than that of the ventricles, but the quantity of blood which they contain, is sufficient to distend the ventricles, as these are partly filled by blood flowing through the auricles into them, before the occurrence of the auricular systole.

The *force* of the *auricular contractions* cannot be measured. From observations on the blood-pressure in the *arteries*, the force of the *left ventricle*, is estimated to be equal to about $\frac{1}{50}$ th part of the weight of the entire body; whilst that of the *right ventricle*, is supposed to be less than half that force. The difference in the average thickness of the walls of the two ventricles, which is about as 3 to 1, affords one ground for estimating the difference in their power.

The dilatation of all the cavities of the heart, is, at least chiefly, an intrinsic or spontaneous act, and not simply a passive distension, caused by the blood flowing from the veins into the auricles, or by that forced by the auricles into the ventricles; for when the heart of an animal is removed from the body, or even when its auricles are separated from the ventricles, both sets of cavities not only contract, but dilate. In neither of these conditions, however, does any internal pressure, or dilating force, act upon their interior, like the blood in the living state; the cavities of the heart must therefore dilate spontaneously, owing, as already mentioned, to the relaxation of their previously contracted muscular walls. This dilatation assists the entrance of blood into them, by diminishing the resistance to the passage of that fluid; it thus saves the waste which would occur in the employment of a special dilating force.

The heart in Man, as observed in the case of beheaded criminals, beats only a few minutes after their execution; this is also true of the warm-blooded animals. Its contractions continue much longer, after systemic death, in cold-blooded and hybernating creatures. The actions of the heart become slower and irregular, ceasing last in the right auricle, the so-called *ultimum moriens*. They are stimulated by heat, the injection of fresh blood, the action of oxygen, and by galvanism; they are arrested by carbonic acid, sulphuretted hydrogen, the vapour of chloroform, and also, after a time, in a complete vacuum.

The beats of the heart, recurring at more or less regular intervals, exhibit an example of so-called *rhythmic* action; their rhythm, like that of the respiratory movements, is, indeed, very remarkable. The cause of this rhythm was, at one time, supposed to be the stimulation of the inner surface of the cavities of the heart by the blood, and it was further imagined that some relation might exist between the special irritability of the right side of the heart, and the qualities of the dark or venous blood returning from the body, and also between that of the left side of the heart, and the qualities of the red or arterial blood entering them from the lungs. Moreover, the ventricles, stimulated to contract by their contents, were supposed, after forcing the blood through the body and lungs respectively, to accomplish the filling of the auricles; the contraction of these, excited, in a similar manner, by their contents, was supposed once more to fill the ventricles, and so on. The muscular walls of the heart, undoubtedly possess great irritability, even in a warm-blooded animal; the inner surface of the auricles and ventricles, is also both sensitive and excitable, and is certainly more rapidly acted on by poisons than their outer surface. (Henry.) But the heart, or even a separate portion of that organ, taken from a hibernating warm-blooded, or from any cold-blooded Vertebrate animal, may not only retain its general irritability for days, but may continue, for a time, to perform *rhythmic* contractions and dilatations, even if removed from the body, though no blood is left in it, and though freed from the stimulus of oxygen, as when placed in a vacuum. The frog's heart will beat thus for twelve hours. Although, therefore, the rhythmic motions of the heart in the living animal, may be partly due to the stimulus of the blood entering its cavities, yet this cannot, under all circumstances, be the cause of such rhythmic actions.

Through the pneumogastric nerves, the *cerebro-spinal* nervous centres, as shown by experiment and by observation in disease, greatly influence the heart's action, under some circumstances, increasing, and, under others, lowering or inhibiting it (vol. i. p. 389); but there is no evidence of their being the cause of the rhythmic character of its movements. The action of the heart is influenced by the emotions and passions, and, according to some, even by the will. In the celebrated case of Colonel Townsend, recorded by Cheyne, the breath could be held, and thus the movements of the heart could be controlled by an act of the will. The heart is excited or depressed by various diseases of the brain, as by cerebral inflammation on

the one hand, and by apoplexy on the other; and its action is disturbed, or even abruptly suspended, by severe injury or destruction of the brain or spinal cord, or of these two parts of the nervous centres together. These and other phenomena of a similar kind are due to excitement or shock, and their effects are often more or less transitory. The *sympathetic* nervous centres, and the cervical parts of the spinal cord with which they are connected, also influence the movements of the heart, as is shown by experiments, and by the effects of blows on the abdomen, or of other injury, or disease (vol. i. p. 391). But if the injury, either to the cerebro-spinal or sympathetic system, be gradually inflicted, the heart's movements will continue, even although the brain and spinal cord be removed, particularly if artificial respiration be performed. From these facts, and especially from the circumstance that the rhythmic movements continue after the removal of the heart, it is evident that the regulating agent of these movements, is not in the great nervous centres, but somewhere in, or upon, the heart itself. It is now admitted, indeed, that the numerous sympathetic ganglia, connected with the nerves upon the heart, are the sources of the stimulus or force which excites the rhythmic contractions of its muscular fibres. In the hearts of the frog and tortoise, these ganglia are chiefly found near the junction of the auricles and ventricles, in the neighbourhood of the auriculo-ventricular openings. If the heart of one of these animals, be removed from the body, and be divided *longitudinally* into its right and left halves, the auricle and ventricle in each half will still continue to contract and dilate rhythmically; if, however, the heart be divided *transversely*, below the base of the ventricles, so that a larger or smaller portion of the ventricles is detached from the rest of the heart, the auricles and the base of the ventricles which are connected, continue to contract rhythmically. But the separated piece of the ventricles, no longer does so, although isolated and spreading contractions may still be excited in it, by the application of a mechanical or other stimulus. By yet further sections, the regulating agent of the rhythmic action, is shown to be confined to the immediate neighbourhood of the auriculo-ventricular orifices, or to the line of junction between the auricles and ventricles, in which part the chief ganglia are found. The synchronous combination of the auricular and ventricular motions on the two sides, may be due to connections between the several ganglia. These local cardiac ganglia must be regarded as

nervous centres, which originate a co-ordinate and rhythmically exerted energy, stimulating the muscular fibres of the auricles and ventricles to perform their characteristic movements, in regular and periodic succession. It has been suggested that these nervous centres exert, or discharge, such energy rhythmically, or at periodic intervals, owing to a periodicity in their nutritive processes, by which they alternately accumulate and discharge the nerve force necessary to excite the muscular substance of the heart (Paget). Why this periodicity of nutrition occurs, is still unexplained.

It has been supposed that the condition of the blood distributed to the substance of the heart itself, may, in some way, determine its rhythmic actions, either the presence of dark venous blood in its capillaries directly stimulating the muscular contractility (Brown-Séquard), or the absence of oxygen acting in a similar manner (Radcliffe).

When the heart of a cold-blooded animal is removed, irritation of any part of it, is propagated to the rest, and rhythmic contractions are set up; but if the heart be partially divided, the effects of the irritation may be still conducted along muscular parts, but not along the tendinous structures. In the entire heart, when removed, the auricular contractions always begin at the sinus; this fact, and also the successive actions of the auricles and ventricles, justify the comparison of these movements, to the progressive peristaltic motions of the œsophagus and intestines. When a ligature is applied around the entrance of the *venæ cavæ* into the right auricle, the auricles and ventricles remain for a time distended, but the sinus continues to contract.

The *frequency* of the beats of the heart, as indicated by the impulse against the left side, and by the pulse, averages, in a healthy adult, about 70 in a minute; but in the male, it is below, and in the female, above that number. The frequency of the heart's beats, and therefore of the pulse, is modified, however, by many circumstances. It is affected by the stature, being slower in tall, and quicker in short persons. The influence of sex just indicated, may possibly be due to the accompanying difference in stature; the difference in the sexes ranges from 10 to 14 per minute. Age has a still more remarkable effect. Thus the pulse is quicker before birth than after. In infancy it is very rapid, and it gradually diminishes in frequency as life advances. It is said, however, to be somewhat slower in infants under six months of age,

than after that period, and also to become quicker again in extreme old age :—

Frequency of the Pulse at different Periods of Life.

Periods of Life	No. of Beats per Minute
Before birth	150
At birth	140 to 130
First year	130 „ 115
Second „	115 „ 100
Third „	100 „ 90
Seventh „	90 „ 85
Fourteenth „	85 „ 80
Adult life	75 „ 65
Old age (above 70)	80 „ 75

Temperament and idiosyncrasy modify the number of the heart's beats, which are fewer in phlegmatic, and quicker in sanguine and nervous persons. The heart beats more slowly in sleep, and more quickly during excited states of the mind or body; the depressing passions lower the number of its beats, or even arrest its movements altogether. Disease sometimes, as in fever and inflammation, increases the frequency of the heart's action, or, as in compression of the brain and in apoplexy, diminishes it. Loss of blood, when gradual and moderate, diminishes the frequency of the heart's beats; whilst sudden or excessive hæmorrhage increases them. The effect of taking food, is to accelerate the heart's action, animal food producing a more immediate effect, and vegetable food a more lasting one: warm food acts more quickly than cold. The effect of alcoholic and other stimulants is well known, and is indicated by their title. It is alleged, that the pulse is more accelerated after breakfast than after dinner. Abstinence and starvation lower its frequency, so also does the prolonged use of a vegetable diet, or the drinking copiously of water. Muscular exertion increases the number of the heart's beats, an alternate contraction and relaxation of the muscles, having a greater effect than a continuous contraction; it also increases the respiration. Posture has a remarkable influence, evidently dependent on the muscular effort expended in maintaining different positions of the body; thus, the beats of the heart are slowest in the recumbent, somewhat quicker in the sitting, and most frequent in the standing, posture. The increase per minute, produced by the change from the recumbent to the sitting position, is 6, and from the latter to the standing posture 9 more, i.e. a difference of 15 occurs between

the lying and standing positions. The effect of posture is greater in the morning than in the evening, and it is greater also when the pulse is quick than when it is slow, the difference resulting from the change between lying down and standing being 9 only, when the pulse is 60, 15 when the pulse is 80, and 27 when the pulse is already 100 (Guy). That the increase in the heart's beats, from change of posture, is due to muscular effort, is shown by placing a person in the recumbent position on three chairs, and then removing the central one, when the pulse immediately rises, although the horizontal position is still maintained; whereas, in a person fastened to a revolving board, and moved into the erect posture, without effort of his own, no such elevation of the pulse takes place. The frequency of the heart's action undergoes changes coincident with the seasons, being greater in spring and summer than in autumn or winter. The rapidity of the heart's action, is also influenced by the hour of the day, being always quicker in the morning, and somewhat retarded towards evening, other conditions as to health, food, and the state of the body being equal; this difference depends, doubtless, on the gradual exhaustion of the powers of the system during the day's work, and on the recovery of power by the rest obtained at night; it may partly explain, why the pulse is more accelerated after breakfast than after dinner. During fasting, the pulse exhibits three periods of increased rapidity, and three periods of descent in the twenty-four hours; thus, it rises from midnight to 2 A.M., from 10 to 11 A.M., and from 2 to 6 P.M.; whilst it falls from 3 to 4 A.M., from 1 to 2 P.M., and from 6 to 8 P.M. The joint effect of the time of day and of food, is illustrated by the fact that the pulse, though progressively decreasing from two hours after breakfast to from 3 to 5 in the morning, exhibits fluctuations after each meal, so that four maximum, and four minimum, points are noticeable daily. The difference between the highest and lowest points, varies from fourteen to thirty-four pulsations. The minimum points are all observed before meals, the maximum points about two hours afterwards, the greatest increase being after breakfast. External temperature and its concomitant effects on the body, also influence the beats of the heart most materially, an elevation of temperature increasing, and a gradual lowering of the temperature diminishing, their frequency, as is illustrated by the exciting effect of a warm bath, and by the influence of long continued exposure to cold; but the sudden and brief appli-

cation of cold, accelerates the beats of the heart. Elevation above the level of the sea—in other words, a diminution of the atmospheric pressure—is found to increase the beats of the heart; thus, Dr. Frankland, whose natural pulse is 60, found that after six hours' sleep on the summit of Mont Blanc, thus excluding the effects of recent muscular effort, his pulse was 120 per minute; on reaching, in the descent, the so-called Corridor, it was 108; at the Grand Mulet it was 88; and at Chamounix it was 56. As one effect of high elevation, is to increase the frequency of the respiration, in consequence of the greater tenuity of the atmosphere, and, as a relation exists between the frequency of the heart's action and the respiratory movements, the increased rapidity of the pulse in elevated positions, may thus be partly explained. An increase in the density of the atmosphere, such as takes place in a submerged diving-bell, is said to lower the frequency of the pulse, and also the movements of respiration. An increase of barometric pressure of $\frac{1}{5}$ th of the normal pressure, lowers the pulse, on an average, ten beats per minute, whilst the respirations are simultaneously lessened by two. (Vivenot.)

The normal relation between the number of respirations and the heart's beats, is, on an average, 1 to 4; in diseased conditions, this ratio is often interfered with, but it is preserved in those accelerations or retardations of the breath and pulse, which take place in the healthy state, such as those due to exercise, change of posture, food, stimulants, and emotion, or to the opposite conditions of rest, abstinence, or depressing influences. Thus, if the normal respirations were 16 per minute, the pulse would be about 64; and if the former were increased to 18 or 20, the latter would be raised to 72 or 80. Expiration diminishes, and inspiration increases, the frequency of the pulse.

A certain relation appears to exist between the facility or the difficulty of the capillary circulation, and the rapidity or slowness of the heart's action: and this may explain some of the preceding phenomena. Thus, the application of cold to the surface of the skin, limiting or checking the circulation through the systemic capillaries, by contracting the small arteries, is accompanied by a retardation of the heart's beats; a state of repose acts, but less powerfully, in the same way. A feeble and slow respiration, lessening the capillary circulation through the lungs, has a similar effect; so also has holding the breath. On the other hand, exercise and heat

quicken the systemic capillary circulation, and also increase the frequency of the ventricular systoles, and so does a quickened and active condition of the respiration. Any obstacle to the flow of blood through the vessels, and thereby to the action of the ventricles, appears therefore to be sympathised with, and a reduction of the heart's beats is the result; whilst the removal of such obstacle is followed, in like manner, by the greater rapidity of the beats. Exercise, excitement, and food, probably, also act on the heart, by producing a greater flow of blood to that organ.

Not only the frequency, but the *force* of the heart's beats, may be modified by external or internal circumstances. This force is increased by all those conditions which may be characterised as stimulating or strengthening, such as exercise, food, stimulants, repose, and so on; whilst depressing and weakening conditions, on the other hand, lessen its force. Stimulating medicines, such as ammonia, ether, and alcoholic preparations, increase the force and frequency of the heart's beats; whilst sedatives, and especially digitalis, diminish their frequency, the latter drug not lessening the force. The *impulse* of the heart, generally proportional to the strength of the body, is affected by various conditions; it is least felt in the recumbent position, on the back or on the right side, and most distinctly in the prone position, or when lying on the left side; in the upright posture it is moderately strong. The impulse of the heart is less manifest in stout persons, but much more evident in thin ones; it is also more perceptible during a forcible expiration, and less so during a powerful inspiration, because, in the latter case, the heart is overlapped by the inflated lung, whilst in the former, it approximates closely to the walls of the chest. It is also increased by exciting causes, such as exercise, food, stimulants, and certain emotions which produce the so-called perceptible impulses constituting *palpitation of the heart*. As already mentioned, the rhythm of the heart may be interfered with by causes acting through the nervous system, in which case, it may even become irregular, so that successive beats of the heart take place at unequal intervals of time, or certain beats may altogether intermit.

Lastly, the force, rhythm, impulse, and likewise the sounds of the heart, are variously modified by morbid conditions of that organ and the adjacent parts, as by thickening or hypertrophy, thinning or atrophy, of its walls, thickening and imperfect closure of, or irregular growths on its valves, adhesion of the

pericardium to the heart, or the presence of membranous deposits or fluid between it and that organ. The impulse and sounds may even be altered by affections of the lungs, pleura, or thoracic walls. The morbid changes in the sounds of the heart, are distinguished by terms descriptive of their character, position, cause, or period of occurrence. Thus, there are murmurs blowing or rasping, and friction sounds; mitral or tricuspid sounds; aortic or pulmonary; regurgitant or constrictive; diastolic or systolic. The most marked and frequent murmurs are the mitral regurgitant, from imperfect closure of the mitral valve, and the aortic constrictive, from narrowing of the orifice of the aorta. General enlargement of the heart, increases the area of local dulness on percussion of the chest, due to the contrast between the solid heart and the inflated lung. Fluid effused into the pericardium, also increases the dulness; but, moreover, it weakens or gives a distant character to the heart's sounds. Drier and solid effusions, as of lymph, cause a peculiar pericardial friction sound, or even tremors which may be felt in the thoracic parietes, dependent on a rubbing together of the surfaces of the heart and its pericardial sac.

Motion of the Blood through the Arteries, and influence of those Vessels on the Circulation.

The phenomena of the circulation of the blood through the arteries, have been studied exclusively in the systemic arterial vessels; for the pulmonary arteries and their branches are removed from direct observation and experiment. The structure and distribution of the arteries, the properties of their coats, and their mode of subdivision and anastomoses, already described (vol. i. pp. 18, and 57), have important influences on the motion of the blood through them. The very smooth, glassy surface of the internal coat, serves, like that of the endocardium of the heart, to diminish the friction between the blood and the sides of the bloodvessels.

The remarkable physical property of *elasticity*, possessed by the middle arterial coat, is of extreme importance; it exists in a more striking degree in the larger arteries, especially in those near to the heart; it is manifested not only on stretching the vessel in a lateral, but also in a longitudinal direction. Two purposes are served by this elasticity; first, it protects the arteries against the force of the heart, to which they yield,

instead of offering a rigid resistance; and, secondly, it enables them to recoil, after they have thus yielded, and to react upon the column of blood within them. It is this recoil which gradually converts the intermittent force of the heart, into a continuous pressure in the small vessels. Moreover, the elasticity of the arteries enables them to bear occasional increase in the quantity of blood forced into them from the ventricles, as in conditions of excitement; or a more permanent addition to the normal quantity, as in plethora. Lastly, it prevents their compression by the ordinary muscular movements, and permits them to bend and elongate, and so to accommodate themselves to changes of position in the trunk and limbs.

The *vital contractility* of the involuntary muscular arterial walls, is of equal importance. Contrary to what is the case with their elasticity, this contractility is feebly manifested by the larger arteries, but is very active in the smaller ones. This property of the arteries, is shown by their slow contraction after death, owing to which, when no longer distended by the force of the heart, they contract, and are usually emptied of blood; also by their contraction under the influence of cold, heat, and mechanical, chemical, and electrical stimuli, applied either to themselves, or to their nerves. Like the contractility of the other muscular fibres of organic life, that of the arteries is slow in its manifestation. Different stimuli, however, act differently in exciting it. Some are said to cause slow contraction, and others, a more rapid contraction, with subsequent slow return to the natural state; some speedily produce marked dilatation, and others, a dilatation, followed slowly by a persistent condition of contraction. The stronger the stimulus, the more likely is it to produce this latter effect. The tonic contraction of an artery is powerfully excited by cold; whilst warmth relaxes it; but a caustic heat causes the most durable contraction, which may, in part, explain the effect of the actual cautery in arresting hæmorrhage. John Hunter demonstrated the existence of this contractility in portions of the moderate-sized arteries, which, he showed, went on contracting, for a time, after death, by a sort of *rigor mortis*, and then dilated again, owing to the resiliency of the elastic coat. Poiseuille found that, after subjection to an equal distending force, an artery, which still retained its vital contractility, contracted more than a perfectly dead one; he also observed that when a living artery was injected with a certain force, it recoiled with a *greater*

force, a result implying more than the reaction of mere elasticity, which could only be equal to the original force. The vital contractility of the smaller arteries, has been demonstrated in the mesenteric arteries of toads and frogs, by means of cold (Schwann), by the application of magneto-electricity to the frog's web (Weber and Kölliker), and in still smaller vessels in the mouse, bat, and frog, by various chemical, irritant, and mechanical stimuli (Wharton Jones, Lister, and many others). Weber found that minute arteries begin to contract in two or three seconds after stimulation; in five to ten seconds, they are diminished to half their original area, and, the stimulus being continued, become completely closed, after which, the electrical current being removed, they slowly dilate again to their original size. The vital contractility of the arteries, may be excited through the nervous system, either directly, or in a reflex manner; for they undergo changes in diameter, through the contraction or relaxation of their muscular coat, induced by division or irritation of the vasi-motor nerves or nervous centres (vol. i. p. 389). Two purposes are fulfilled by this vital contractility of the arteries; first, that of slowly adapting the capacity of the entire arterial system, to the quantity of blood circulating through it; and, secondly, under the control of the nervous system, that of modifying the relative quantity permitted to flow to any given organ. Moreover, if, during life, a small artery be cut quite across, its contractility closes its orifice, and so arrests further hæmorrhage. This fact, indeed, is quoted as a proof of its contractility; for the elasticity of the arterial walls is insufficient to account for the perfect contraction of a wounded vessel, and would rather tend to keep it partly open, as we see happens in a dead artery.

It has been supposed that the contractility of the arteries might serve, as well as their elasticity, to adapt them to the intermittent and variable pressure of the blood projected into them by the heart; but there is no evidence of this, and the characteristic slowness of action of organic muscular fibres, renders it doubtful whether the arteries could alternately relax and contract, concurrently with the rapid action of the heart.

The so-called *tone* of the arterial system, seems to depend on a healthy contraction of the muscular coat—the so-called property of *tonicity* being a continued exercise of muscular contractility. This tonicity is shown by the contraction which

takes place in the portion of an artery included between two ligatures, when it is punctured to allow of the escape of its contained blood; also by the gradual emptying of an arterial trunk beyond any point at which it has been tied—a contraction much more complete than elasticity can explain; and, again, by the almost complete obliteration of the canal of a portion of artery removed from a living animal, and subjected to continued cold. The elasticity of the artery, is, however, also, incessantly at play in the natural state of the vessel, which is always in a condition of moderate and constant tension, permitting and explaining its slight contraction and retraction into its sheath, when it is divided.

As already stated, by the successive contractions of the ventricles, and by the closure of the auriculo-ventricular valves, the blood is not only directed from the heart into the great arterial trunks, but is also projected into them by successive jerks. If the arteries had rigid inelastic walls, this intermittent motion of the blood in them, would be propagated even to the capillary system. Owing, however, to their elasticity, and to the successive closure of the semilunar valves across the mouths of those vessels, the separate impulses caused by the ventricular contractions, are gradually rendered less distinct, and, finally, before the stream of blood enters the capillary vessels, its motion becomes continuous. The elastic coats of the aorta, near the heart, having been distended by the force of the left ventricle, recoil on the contained blood; this fluid being practically incompressible, transmits the pressure on itself, *backwards*, so as to close the semilunar valves, and *forwards*, so as also to urge onward the column of blood in the systemic arteries. But the intermittent effect of the heart's strokes, is propagated onwards through all the main arteries of the body, in which it is manifested by the pulse, and by the escape of the blood *per saltum*, or in jets, from any of those vessels when they are wounded. The motion of the blood from the ventricle, is truly intermittent—that is, it ceases absolutely at intervals; the jet from a large artery, when wounded, is not quite intermittent; that from the smaller arteries, though the stream is jerking, is distinctly *remittent*, i.e. the jet never ceases altogether, but is alternately stronger and weaker; finally, in the smallest or microscopic arteries, the flow of the blood, under ordinary circumstances, loses even the remittent character, and becomes perfectly equable and continuous, and remains so in the capillary vessels. This

effect of the elastic recoil of the previously distended arterial walls, may be illustrated by the action of a vulcanised india-rubber tube, which, if of sufficient length, changes the jerking flow of water, forced into it by a syringe or pump, into a flowing stream. The force of the ventricle, transmitted through the column of blood, acts most powerfully on the vessels nearest to the heart, in which the elastic tissue is most abundant; whilst the effect of the ventricular force is gradually weakened in the more distant vessels, the elastic coat of which becomes proportionally thinner. On the contrary, as already mentioned, the muscular fibres are relatively least abundant in the largest, and most so in the smallest arteries; and it is improbable that their contractility is called into play, to resist the distending effect of the heart's force. Although the arteries, by their resilience, at length convert the intermittent stroke of the heart into a uniform propulsive force, yet the heart itself is still the moving agent of the arterial blood; for the recoiling force exercised by the arteries, is itself due to their previous distension by the force exerted by the heart. When, indeed, this force is too weak to distend the arteries as usual, the remittent flow, or jerking escape of the blood, is observed in the most remote arteries, not only in those next to the capillary vessels, but even in the capillaries themselves. The elasticity of the arteries engenders no new force in the circulation, but utilises that of the heart. Without it, the force of this organ would probably rupture the microscopic arteries, or the capillaries, of many delicate structures, and so give rise to internal hæmorrhages or apoplexies; such accidents, indeed, occur when the coats of the arteries are converted, by disease or degeneration, into more or less rigid tubes. Besides acting in the distension of the coats of the arteries, a certain part of the heart's force is lost, being propagated, by disturbance of those vessels, to the neighbouring hard or soft tissues.

The frequent branchings and bendings, and especially the anastomoses of the arteries, or their communications with one another, as they approach the organs to which they are distributed, as well as in the interior of those organs, serve to diminish, as well as to equalise, the force of the heart's action. The multiplication of the smallest arteries, and, therefore, of their points of entrance into certain delicate organs, as seen in the ciliary arteries of the eyeball, and in the pia-mater of the brain, must also lessen the pressure upon each of them.

Moreover, the frequent anastomoses of the arteries, as in the vicinity of the joints in the limbs, and especially at the base of the brain, serve to secure a due and constant supply of blood to a given part through certain vessels, when others are temporarily obstructed by external or internal pressure, or permanently interrupted by aneurisms, tumours, or accidental division of the ligature of an arterial trunk. Anastomosing branches given off above and below the seat of ligature, gradually, or even rapidly, enlarge, forming large collateral vessels, through which the so-called *collateral circulation* is carried on. Such enlargement of an artery is due, not to a mere relaxation of its coats, and consequent dilatation, but to an increased nutrition of its walls, by which it undergoes a positive enlargement; in like manner, arteries which are no longer traversed by blood, though, in the first instance, they merely contract, afterwards become reduced in size, by a positive atrophy or absorption of their coats.

The *supply* of blood to a given organ, depends primarily upon the size of the main artery distributed to it; but secondarily also, upon the rate of motion of the blood through those vessels, which varies, as we shall see, according to many circumstances. But, as previously mentioned, the calibre of the arteries, especially of the smaller ones, is not constant; for it undergoes changes in accordance with the state of relaxation or contraction of their muscular coat, being sometimes of normal size, and sometimes larger or smaller than usual. The increased redness of the cheeks in blushing, or that of irritated and inflamed parts, depends partly upon a temporary change in the calibre of the smallest arteries, which are then manifestly dilated. Hence the supply of blood to a part or organ, may also be regulated by the contractility of its arteries, which is itself controlled by the nervous system.

The *rate of motion* of the blood in the arteries, has been calculated from observations made upon animals. Two kinds of instruments have been employed in such observations. One, the *hæmadromometer* of Volkmann, consists of a bent U-shaped glass tube, having its ends fitted into a short, straight, hollow metallic mounting, placed at right angles to it. By means of stopcocks, a free passage can be maintained, either through the straight portion of the apparatus only, or through the bent U-shaped part. When the two ends of the straight portion of this instrument, are fastened into the cut ends of the divided carotid artery of a dog, the arterial blood-current may either

be allowed to flow through the straight portion, or it may be suddenly diverted, by changes in the stopcocks, through the bent or U-shaped part. The rate of motion of the blood through the latter, being observed, and the length of this tube being known, the velocity of the blood-current is ascertained. Another instrument, the *hæmatochometer* of Vierordt, is composed of a small square box or cell, made with glass sides, filled with water, and having an aperture of entrance and one of exit, each fitted with a tube; to these tubes, the cut ends of a divided artery are attached. Within the box, is a fine pendulum, carrying, in order to aid the observation of its movements, a disc of silver, which, when the pendulum is at rest, hangs close to the aperture of entrance. A curved graduated scale is marked on the side of the vessel. When the arterial blood is permitted to flow into this box, it raises the pendulum with a velocity corresponding with that of its own motion, and which is at once measured by the graduated scale. According to Vierordt, the mean velocity of the blood in the carotid of a horse is 11·7 inches, of the dog 10 inches, and of the calf 9 inches per second; the calculated velocity in the aorta of the horse, is 12·5 inches, and in the human carotid, rather more than 10 inches per second. According to Volkmann, the velocities for the carotid artery in these animals, are a little higher; but in the metatarsal artery of the horse, only 2·2 inches per second. By means of the *tachometer* of Chauveau, a modification of Vierordt's instrument, it is shown that a great difference in the velocity of the blood-current, exists during the systole and diastole of the left ventricle; for during the systole, in the horse, the velocity is about $20\frac{1}{4}$ inches, and during the diastole only $8\frac{3}{4}$ inches per second. The velocity of the blood in the arteries, is, moreover, diminished during inspiration, and increased during expiration.

From the preceding figures, it appears that the rate of motion of the blood in the arteries, is quickest near the heart, gradually becoming slower in the more distant vessels. First, the effect of the heart's action is diminished by the resistance offered, by friction and adhesion, to the passage of the blood through the arteries and capillary vessels; this frictional resistance, though rendered as slight as possible by the smooth lining membrane of the arteries, is increased by the curvature, by the angular bending, and by the frequent subdivision, of the arteries, by an unusual rigidity of the walls of the arteries, and by any alteration in the viscosity of

the blood, or in its nutritive attractions for, or relations with, the capillary walls and the tissues beyond them. All these conditions, therefore, tend to retard the velocity of the blood-current, by an increase of resistance and friction. Secondly, the force of the heart, and therefore, the rate of motion of the blood, is wasted by the slight loss from friction between the particles of the elastic coat of the vessels, occurring in their distension and recoil, and likewise by the disturbance of the artery and the surrounding tissues. Lastly, an efficient cause of retardation in the arterial blood-current, is the obvious increase in the total capacity of the branches of the arteries, as compared with that of the trunks from which they arise; for not only do the united *diameters* of two or more branches, exceed the diameter of the parent trunk, but, though of course in a much less degree, the combined *areas* of two or more branches, are usually larger than the area of the parent trunk. The combined areas of the two iliac arteries, into which the abdominal aorta divides, are, however, larger than that of the aorta itself. Opening an artery, which not only causes hæmorrhage, but also diminishes the resistance in the arteries, increases the velocity of the blood in the opened vessel: this result may be exhibited by experiments with artificial tubes injected with water, and then opened.

The *force* of the heart, or the blood pressure, in the arteries, has been frequently investigated, both by the earlier and later physiologists. Stephen Hales found that, on fitting a long tube containing water, into the crural artery of horses, the force of the blood-current was sufficient to elevate the water in the tube, to heights varying, in different cases, from 8 feet 3 inches to 9 feet 8 inches. From these and other experiments, he inferred that the pressure of the blood in the large arteries of the human body, would support a column of blood 90 inches, or 7 feet 6 inches, high, or a weight of 3 pounds 7 ounces per square inch. More recently, Poiseuille invented the *hæmadynamometer*, a much more convenient instrument, in which a short column of mercury is substituted for the longer column of water in Hales's apparatus. This instrument, as now improved, and named a *manometer*, consists of a U-shaped glass tube, having one of its stems or legs longer than the other; the shorter leg is bent horizontally, and provided at its end with a stopcock, and with a piece of elastic tube, so that it can readily be adapted to the cut end of a divided artery in a living animal. The lower curved

part, and 3 or 4 inches of both legs of the U-shaped tube, are filled with mercury, and the space in the short leg, between the surface of the mercury and the stopcock against which the artery is fixed, is occupied with a solution of common salt, sulphate of soda or Glauber's salt, or carbonate of soda, so as to prevent the coagulation of the blood when it enters the apparatus. At the back of the tube, is fixed a graduated scale, the zero of which corresponds with the level of the mercury when at rest in both legs. When the horizontal part of the short leg of this instrument, is connected with an artery, and the stopcock is opened, the apparatus being maintained in a vertical position, the force of the blood-current depresses the mercury in the shorter, and raises it in the longer leg. The difference between the level of the mercury in the two legs, gives the height of the mercurial column supported by the blood pressure. But the level of the mercurial column in the longer leg, is very inconstant; for it is raised at each ventricular systole, and lowered at each diastole: the highest point indicates the full power of the heart, overcoming the resistance of the column of blood, and distending the arterial walls; whilst the lowest point shows that force, reacting through the resilience of the arteries only. The mean height between the two levels, is usually recorded as the average blood pressure. Hales had already noticed, in his apparatus, a descent of 1 inch in the blood column, between each pulsation. To determine the exact force in pounds weight, the difference between the sectional area of the artery experimented upon, and that of the tube containing the mercury, must be noted, and the weight of a mercurial column of the indicated height, but of the same area as the artery, must be determined by calculation. Should any blood descend into the tube, its weight must be reckoned, though it is only $\frac{1}{16}$ th the weight of mercury.

By means of a simple hæmadynamometer, Poiseuille found that the blood pressure varied little in different sized arteries, and in different sized animals; and he concluded that 6·3 inches of mercury was, in all cases, the average equivalent of pressure. This general result corresponds nearly with that calculated by Hales for Man; thus mercury being 13·6 times heavier than water, 6·3 inches of the former would be equal to 85·68 inches of the latter, Hales's estimate giving 90 inches of blood, which are equal to 95 of water. Again, 6·3 inches of mercury on the square inch, would be equal to 3 lb. 2 oz. pressure, Hales's estimate being equal to 3 lb. 7 oz.

The force of the left ventricle itself, can only be estimated from that observed in the arteries nearest to the heart; taking the blood pressure in the aorta, at 6·3 inches of mercury, then the force of the left ventricle is found by multiplying that number by the square inches contained on the internal surface of that cavity.

The uniformity of pressure believed by Poiseuille, to exist in arteries, both near to and distant from the heart, which was thought to equalise the force of the circulation in every part, and so to render congestion or deficiency of blood, ordinarily impossible, does not appear to prevail. In a system of rigid tubes, the pressure would be uniform, unless these were of very great length, and then only from friction. In curved and resilient tubes, however, branching into vessels of rather larger area than the trunks, some loss of force must be sustained. Neither is it true, as Poiseuille supposed, that, in a series of animals of different size, the blood pressure in the arteries is nearly uniform, because, as he alleged, it is regulated by a relation between the force of the ventricle, and the size of the aortic orifice.

An adaptation of the hæmadynamometer, named the *kymographion*, which yields very accurate results, has enabled more recent experimenters, to correct the observations and conclusions of Poiseuille. Upon the surface of the mercury in the longer leg of the ordinary instrument, there rests a float, which is made to carry a vertical rod; on the upper end of this, is fixed a horizontal pencil, having its point resting on a drum capable of revolving upon a vertical axis. When the instrument is in use, the drum is made to turn at a given rate, by clockwork, and the pencil, moved by the mercury, describes a waved line corresponding with the variations in the blood pressure. In this way, the pressure is shown by Ludwig, Volkmann, and others, to vary in animals of different size, and, in the same animal, in arteries at different distances from the heart, as well as according to different states of the circulation, respiration, and nervous system. Thus, in the horse the average blood pressure was nearly 11 inches; in the dog, nearly 6 inches; in the rabbit, as a mean, rather more than 1 inch; and in the frog, rather less than 1 inch. Again, in the carotid of the calf, the pressure was equal to $4\frac{1}{2}$ inches of mercury; but in the metatarsal artery to only $3\frac{1}{2}$ inches. Lastly, in medium-sized animals, the blood pressure varies from $\frac{1}{5}$ th to $\frac{2}{5}$ ths of an inch in the larger vessels. According to other

authorities, it differs much more than this, even in the same artery. Moreover, there are slight fluctuations, due to the state of the respiration, to hæmorrhage, starvation, muscular effort, and other causes, implying variations in the force of the heart, either increase or diminution. The pressure is weaker in younger animals. In the pulmonary arteries, the pressure is only equal to from $\frac{1}{2}$ to 1 inch of mercury; but the abnormal disturbing effects of opening the thorax cannot be accurately estimated (Ludwig).

The force of the blood-current in the arteries, or the blood pressure, not only varies between each ventricular systole, and according to the strength of the heart's action in different circumstances; but it is increased by an addition to the quantity of blood already contained in the system, as when blood is artificially injected into the veins; whilst, on the other hand, it is lessened by a diminution in the quantity of blood in the body, as in cases of hæmorrhage.

The influence of the respiratory movements on the pressure of the blood in the arteries, is very complex. *Inspiration*, or breathing in, is usually said to produce a diminution in the arterial pressure, and *expiration*, or breathing out, to cause an increase in that pressure. In explanation of this view, it is stated, that, during the act of inspiration, the blood enters the thorax more readily, and thus relieves the whole vascular system of tension; whilst during expiration, the difficulty offered to the entrance of blood into the chest, increases the tension in the vessels, in the arteries as well as in the veins. According to Vierordt, however, in inspiration, the readier entrance of the blood into the thorax, causes the right side of the heart, and soon, also, the left side of that organ, to become more distended, and the arterial pulse, accordingly, increases in fulness, owing to increased arterial blood pressure, during the course of inspiration; on the other hand, in expiration, from the resistance offered to the flow of blood into the chest, the right side of the heart, and soon, also, the left side, receive less blood, so that the arterial pulse, owing to diminished arterial pressure, becomes, in the further progress of expiration, smaller. With regard to the blood pressure in the arteries, Vierordt, referring to the effects of inspiration and expiration, in filling the heart with blood, states that, in the former act, the blood pressure, though at first lessened, afterwards increases, reaching its maximum at the beginning of expiration, after which it diminishes. These views are further

modified by the researches of Dr. Sanderson, who states that the rise in the arterial pressure begins with the act of inspiration, and continues to increase during expiration. Moreover, by these researches, in which a very large hæmadynamometer and kymographion were used, the respiratory act is shown to consist of a period of action occupying two-fifths, and of a period of repose occupying three-fifths, of the entire act; of the former period, two-thirds are taken up by inspiration, and one-third by expiration. The arterial pressure begins to increase at the commencement of inspiration, and continues to rise during expiration, at the end of which, and during the pause, it gradually subsides. In violent expiration, the vascular tension is increased; but also in the prolonged inspiratory efforts of dyspnœa.

The increased pressure from expiration, is illustrated in the tension, and occasional rupture, of bloodvessels in the act of coughing. It has already been mentioned that the velocity of the blood in the arteries, is slightly increased during expiration, and diminished during inspiration, contrary to what happens in regard to the blood pressure. Indeed all the conditions, connected with increased resistance by friction, which diminish the velocity, increase the blood pressure; whilst those which lessen the friction and resistance, diminish the pressure, and increase the velocity. All variations in the arterial blood pressure, are less marked, when the pulse is more frequent, and also as the arteries become smaller.

A double hæmadynamometer, or *differential manometer*, has been devised by Bernard, by means of which the different degrees of pressure in different arteries, or in the same artery on the two sides of the body, under different conditions, or the different pressure in the arteries and veins, can be very conveniently determined. It consists of a U-shaped tube, the bend of which is occupied by mercury, with a solution of carbonate of soda, above it, in each leg: to the two extremities, the bloodvessels to be experimented on, are attached by suitable pipes provided with stopcocks. When these are opened, if the pressure in the two attached bloodvessels is equal, the level of the mercury in each side of the bend, remains unaltered; but when it is unequal, the mercury falls in the leg connected with that vessel, which has the greatest pressure on its contents. For example, in the two carotids, or two facial arteries, of a horse, the pressure is equal; but if the instrument be connected with one artery near the heart,

and with another more remote, it is unequal. Moreover, when this instrument is connected with the same artery on the two sides of the body, division of the sympathetic nerves on one side, is followed by an elevation of the mercury on that side, indicating a loss of tension in the coats of the corresponding vessel.

The Pulse.

The *pulse* is the well-known beat of an artery, sometimes visible to the eye, if the artery be superficial, but more commonly felt by the finger placed upon the beating vessel. Sometimes the pulse is perceptible to the individual himself, being either felt as a throbbing sensation, or heard, as a noise, when near the ear. The *remote cause* of the pulse, is the force of the heart, for its beats correspond in number with the contractions of the left ventricle. Its *immediate cause*, however, is the momentary distension and recoil of the coats of the artery, propagated, along the vessel from the heart onwards, after the manner of a *wave-motion*, and produced by the propulsion of successive quantities of blood into the arterial system by the left ventricle; and commencing *at the instant of closure of the mitral valve*. The force transferred to these successive quantities of blood, is partly exhausted, in urging on the blood already in the vessels; but the resistance thus met with, as we have seen, diverts the force partly on to the elastic sides of the arteries, and so distends them.

This distension of the arteries occurs first in the aorta, close to the heart, but rapidly follows along the entire arterial system. It consists, not only of a lateral dilatation of the vessels, but also of an elongation. The former change is but slight in arteries which can be subjected to examination, and is too quick to be followed readily by the eye; whilst the latter is much more evident, as in the case of superficial and tortuous arteries, such as the temporals, which may be seen to become more curved during the passage of the pulse-wave along them.

The total amount of dilatation observed during the passage of a pulse-wave along a given length of the carotid artery of a dog, has been measured, by placing the artery in a tube filled with water, and having another fine upright glass tube fitted into it; the elevation of the water in the latter, at each pulse, shows an increase of $\frac{1}{2}$ nd of the bulk of the piece of artery so enclosed (Poiseuille). According to Vierordt, the increase is as much as $\frac{1}{5}$ th. The mechanical effect of this

combined dilatation and elongation, but especially of the elongation, of a living artery, and of its subsequent contraction and shortening, and particularly of the latter, is a movement of the vessel in its bed, a motion which is visible in superficial arteries, especially in thin and aged persons, and which can be rendered more perceptible by placing a small bristle across it. It is this change of place, or *locomotion*, of the artery, which is the chief cause of the pulse felt on placing the finger upon the vessel. The blood itself being practically incompressible, the shock of the heart's stroke upon it, is communicated, almost instantly, throughout the whole blood in the arterial system; but the effect of the distension, or distension wave, which begins in the aorta, near the heart, apparently takes a certain time to be continued onwards, for reasons to be presently explained; hence there is a certain measurable rate in the propagation of the pulse to the distant arteries. This is the theory of Marey. But the rate of motion of the distending pulse-wave, is much more rapid than the motion of the blood particles themselves within the vessels, being about 30 feet per second; whilst, as already stated, the velocity of the blood is only about $10\frac{1}{2}$ inches per second in the carotid, and about $2\frac{1}{4}$ inches per second in the distant arteries. This comparison will serve to impress on the mind, the fact, that the pulse-wave is not caused by the onward motion of the blood, but by a wave-motion induced in the entire column of blood, which operates in its passage, laterally, as well as longitudinally, on the coats of the arteries.

The impulse of the heart nearly coincides with the systole of the ventricles, or, rather, it happens somewhat later than the commencement of the ventricular contraction. Now, the pulse-wave passes along the larger arteries, at the termination of the ventricular contraction, i.e. after the impulse of the heart is felt on the side of the chest; and it takes $\frac{1}{6}$ th of a second to reach the radial artery at the wrist. Nevertheless, the pulse is felt even in the most distant parts of the arterial system, *before* the second sound of the heart is heard, whilst the cause of this sound, is the sudden closure of the semilunar valves across the mouth of the aorta and the pulmonary artery. This fact, as first pointed out by Colt, refutes the following theory of Weber, once so generally adopted, as to the cause of the propagation of the pulse-wave. That physiologist supposed that the aortic semilunar valves, being closed by the backward movement of the blood near them, owing to

the recoil of the walls of the aorta nearest to the heart, acted as a fulcrum, from which the blood was propelled onwards by the yet unused resilient force of the aorta, into more and more distant portions of the arterial system, so as to produce the successive wave-like distension of their coats.

This theory of Weber assumes a minor cause, in place of the greater and true one, viz. only a residual portion of the force originating in the ventricular stroke, instead of the whole ventricular impulse. The closure of the aortic valves is not essential to the phenomenon of the pulse, which occurs before the second sound, when these valves are open. But if the pulse-wave be essentially due to the direct force of the heart, communicated through the arterial blood column acting at the *closure of the mitral-valve*, so the *closure of the aortic semi-lunar valves* is not without effect on that blood column, and on the arteries which contain it. When the pulse is very accurately examined, a subsidiary wave occurs after the principal one, producing the phenomena named *dichrotism* or the *dichrotal pulse*, and this, as will be soon explained, has been referred by some, to the effects of the closure of these valves.

For the investigation of this and other phenomena of the pulse, instruments named *sphygmographs* have been devised. The original apparatus of Vierordt, consists of a long, slender, well-balanced, horizontal lever, or measuring rod, supported, near one end, on a proper fulcrum, and having a short vertical stem projecting downwards from near the fulcrum, and ending in a little button which rests upon the artery. To some part of the lever, near the button, are attached certain contrivances, to secure a true vertical motion, and, at its free end, it carries a short pencil, the point of which rests against an upright cylinder or drum covered with paper. To this cylinder, when the instrument is in action, a known rate of motion is imparted by clockwork; at each pulsation of the artery against the button, the lever rises and falls, and so the pencil describes an up and down line on the revolving drum of paper. In this way, a series of pulsations are recorded by an up and down waved line of a peculiar character. In Marey's improved instrument, and in other still later ones, the delicacy of record is more perfect, the lever is longer and lighter, its motions are steadied by the addition of a slight spring, and the pencil leaves its tracings upon a piece of smoked glass which is moved forwards by clockwork, or upon a coil of paper which is constantly being unwound.

The waved lines traced by such an instrument, show, by the number of the undulations in a given space, the *frequency* of the pulse; by the length of the up and down strokes, the *amplitude* of the pulse movement, or the *force* of the pulse; and by the greater or less inclination of these strokes from the perpendicular, or the horizontal distance between the points of commencement of the upward strokes, the *duration* of the pulse-waves. Besides this, certain variations in the lines indicate other characters, such as firmness, or tremulousness, and so forth. There is, however, one character of the pulse recognisable by the finger, concerning which, the sphygmograph gives information which may be delusive, viz. the *volume of the pulse*, which may be full in very different conditions of the system. A full pulse is usually slow and strong, but it may be quick; on the other hand, a small pulse is generally quick and feeble, but not necessarily so. The pulse is wiry, thready, or small, in hæmorrhage, or on approaching death. In recording the pulse movements, this instrument also indirectly measures the force and duration of the systole of the left ventricle, and the duration of the respiratory movements.

The sphygmograph has been ingeniously employed by Marey to assist in determining the cause of the pulse itself. An india-rubber cylinder, provided with internal valves, is fitted at one end, to a short, and at the other to a long, elastic tube. By alternately relaxing and compressing the cylinder, water, under the direction of the valves, is drawn in through the short tube, and pumped intermittently through the longer one. This latter tube is disposed in three loose horizontal coils, each of which is brought in contact with a separate sphygmographic lever, the pencils of all of which, rest upon a paper, previously ruled with vertical and horizontal lines, and which revolves upon one drum, common to the three pencils. The sphygmographic pencils being placed, at starting, exactly under one another, and the drum being made to revolve, three *horizontal* lines are first simultaneously traced; but when the india-rubber cylinder is repeatedly compressed, so as to inject water by separate impulses into the long tube, thus imitating the ventricular propulsion of the blood into the arteries, undulations, resembling the pulse-waves, travel along the coils of the tube, and move the three sphygmographic levers, the pencils of which record the *moment of commencement*, the *extent*, and the *duration* of the movements occurring at three different points of the tube, by up and down lines of corresponding character

and form. In the first place, the line corresponding with the point nearest to the propulsive cylinder, shows a greater amplitude in its undulations, owing to the greater force of the lateral pressure on the walls of the tube at that point; whilst, in the other two lines, a progressive diminution in the vertical depth of the undulating lines, shows a gradual diminution in the pressure, in proportion to the distance from the agent of propulsion. But what is of more interest in relation to the cause of the pulse-wave, is the fact, that though the commencement of the wave, at each of the three points tested by the sphygmographs, is simultaneous, the nearer wave reaches its highest point, before the others, which reach theirs at progressively later times. This is believed by Marey to happen in the living body, and to explain the apparent retardation of the pulse movement, or distension effect, which is indicated by the pulse itself being felt $\frac{1}{6}$ th of a second later in the wrist than close to the heart, although, from the practical incompressibility of the blood, the shock imparted to it by the left ventricle, must be instantly propagated through the whole of that fluid, in the arteries, just as that of the india-rubber cylinder is through the equally incompressible water.

The phenomenon known as the *dichrotous* pulse, is also detected and studied by the sphygmograph. Formerly, it was supposed to be absolutely the result of disease, or of some grave irregularity; but with more delicate instruments, its presence is often detected even in healthy conditions. It is represented by a slight secondary undulation in the down-stroke of the chief or primary pulse-line. It sometimes occurs, in health, during walking, and is noticeable also in the healthy pulse, whenever, owing to the diminished tonicity of the arteries, and their defective distension, they are in a condition to obey slighter impulses communicated to the blood. In the opposite conditions of a highly tonic or distended state of the arteries, this subsidiary wave motion of the dichrotous pulse, is not perceptible. In abnormal conditions, it is a sign of a relaxed state of the arterial system, or of a loss of blood. According to Naumann, the cause of this dichrotism, is the shock communicated to the blood, at the *instant of closure of the aortic semilunar valves*, which, like the sudden arrest of a fluid by the closure of a tap, produces a shock or jar, which is transmitted back through the whole column. The time of occurrence of the dichrotous pulse, corresponds well with this hypothesis; for whilst the primary pulse movement is

felt *before* the second sound of the heart, the dichrotous wave immediately follows it. It is, however, suggested by Marey, that this dichrotism may be due to the primary wave being checked at the lower end of the abdominal aorta, where that vessel divides into the common iliacs, owing to the fact, elsewhere referred to, that the two iliac arteries are smaller than the aorta from which they proceed, contrary to the general rule, that the area of the branches exceeds that of the parent trunk. At this point, the primary pulse-wave is supposed by Marey, to rebound, and to produce a back wave, which causes the dichrotous pulsation. In support of this explanation, it is alleged, that whilst the pulse is dichrotous in all the arteries arising from the arch of the aorta, it is not so in the femoral arteries and arteries of the lower limbs, along which the primary pulse-wave only travels. But Naumann asserts that the dichrotous pulse-wave diminishes in force, as it recedes from the heart—a fact which would support his view, but be opposed to Marey's; for, in the former case, the wave is supposed to travel outwards from the heart, but in the latter, towards the heart, *i.e.* from the lower end of the abdominal aorta. Another suggestion has been made, *viz.* that whilst a primary wave occurs in the blood, a secondary wave follows it in the coats of the vessels; this opinion rests upon an experiment, in which it was shown that the simple injection of a fluid intermittently into an elastic tube, produces such a double wave.

An ordinary *vigorous* pulse-line, as marked on the sphygmographic paper, consists of a series of up and down strokes, which succeed each other at regular intervals, without any dichrotous wave-line in the down-stroke. But the pulse, as is well known, presents, owing to various causes, many modifications in character, each of which is recorded by the sphygmograph. Thus, by increased frequency of the heart's action, the pulse is rendered more rapid, as in the *quick* pulse, and then the up and down strokes of the sphygmographic line become more crowded in a given horizontal space. Again, the pulse may be augmented in force, as in the *strong* or *pounding* pulse, caused by a more powerful action of the heart, as under the effects of stimuli or mental excitement, and then the length of the up and down strokes is increased. The pulse is sometimes *hard*, as when the tension of the arterial walls is increased, whether from exalted tonicity, from extreme fulness of the vascular system, or from obstruction in the

capillaries, causing an obstacle to the flow of the arterial blood. This may happen either from inflammation of a part, or from the brief application of cold to the surface of the body; the coats of the arteries being already much distended, or their tonic contraction being excessive, the pulse-wave scarcely distends them further; hence the up-stroke is short, nearly vertical, and occupies but little space, whilst the line of descent is gradual and prolonged, marking the slow and difficult recoil of the vessel. Lastly, the *soft* pulse, which is met with in relaxed conditions of the system, or may be produced by hot air or water-baths, depends on a deficiency in the quantity of blood in the arteries, or on a defective state of the tonic contraction. With such a pulse, the up-stroke is long, owing to a greater freedom of play of the elastic arterial walls; the down-stroke is much prolonged, and exhibits a small secondary wave, constituting the dichrotal pulse. Moreover, the horizontal space between the commencement of each up-stroke, is diminished, indicating a greater frequency of the heart's beats, whilst, in the hard pulse, the opposite is the case; for, as already mentioned, a sympathy exists between the action of the heart and the state of the circulation; the number of its beats being diminished, but their force increased, when the capillary system is obstructed, whilst the two opposite states occur, when that system permits the easy transmission of the blood. When a hard pulse depends upon a local cause, such as inflammation, it may be accompanied by an increase in the number of beats; but when upon a general cause, such as the application of cold to the whole body, by a diminution in the number of pulsations.

The absolute duration of each pulse, as measured in time by the number of beats in a minute, is indicated on the sphygmographic paper, by the horizontal distance between the commencement of two adjoining up-strokes. This duration may vary as much as 37 per cent. in a series of beats. It varies most in the slow pulse; for the more frequent the pulse, the more equal are its beats in duration; it is very remarkable in the slow pulse produced by poisoning with digitalis. On comparing the up with the down stroke of each pulse-line, it is seen that, usually, the former has a less horizontal progression than the latter, indicating that the distension or dilatation of the arteries, which is related to the ventricular systole, takes place in a shorter time than the recoil or contraction of the vessel, which is related to the diastole. It was formerly said

that the ratio between them was as 1 to 2; but, in health, the proportion seems to be, in an average pulse, only as 100 to 106; in a quick pulse, the ratio is as 100 to 136; in the slow pulse, as 100 to 80 (Vierordt). The period of dilatation varies more than that of contraction.

The influence of the *respiratory movements* on the pulse, so far as its force is concerned, has already been indicated, in describing the arterial blood pressure (p. 232). The *volume* of the pulse during inspiration, as compared with its volume during expiration, is said by Vierordt to be as 218 to 191. It is now established, by aid of the sphygmograph, that the *force* of the pulse is gradually increased during inspiration, and reaches its maximum during expiration, this fact being indicated by the gradual ascent of the *line of mean pressure*, drawn through the middle of a series of up and down strokes. The tension of the artery, on which the fulness of the pulse inversely depends, is increased during inspiration and up to the end of expiration, the pulse becoming harder and firmer, and the length of the up and down strokes shortened; whilst, after expiration, in the pause, the tension of the vessels is lessened, the pulse becomes softer and fuller, and the up and down strokes of the curves are longer. Lastly, the *frequency* of the pulse is modified during inspiration, not, as is sometimes stated, then becoming slower, but, as shown by Vierordt, increasing in frequency, owing to the more easy supply of blood to the heart; this view is confirmed by Sanderson, who, moreover, points out that this increase of frequency continues up to the end of expiration, as is indicated by the greater closeness of the up and down strokes in the horizontal space representing the period of the inspiratory and expiratory acts, as compared with those registered in the space representing the pause at the end of the latter. The *duration* of each pulse is longer in inspiration than in expiration.

The pulse being ultimately dependent on the heart's action, is necessarily modified in *frequency*, *strength*, and *rhythm*, by all those conditions which influence the number, strength, and rhythm of the heart's beats, such as age, sex, stature, position of the body, atmospheric pressure, state of nutrition, stimulation, and excitement, as already detailed (p. 217). When the heart's action is very feeble, the pulse is said to become more evident in the smallest arteries, being propagated to a greater distance from the heart, even to the capillary vessels. This apparently anomalous result is explained

by the heart's action being then too weak to distend the larger vessels to such a degree as, by their subsequent recoil, to convert the intermittent flow of the blood, into a uniform and equable motion. Want of rhythm in the heart, causes *irregularity* of the pulse. The so-called *intermittent* pulse indicates an ineffective ventricular systole, which is too weak to act on the arterial blood column. It may depend on a deficient supply of blood to the left side of the heart, as well as on debility of that organ. It occurs after long fasting, and is also common at puberty, in old age, and in various diseases. In healthy persons, its duration is somewhat longer than that of a single beat of the heart.

Motion of the Blood through the Capillaries.

The tissues in which capillary bloodvessels are found, and those in which they are absent, their number and size in the various tissues and organs, the varieties in the arrangement of the capillary network, and the structure of their delicate walls, are elsewhere detailed (vol. i. p. 60). The form of the capillary network in different parts, has no relation to the functions of those parts, otherwise than so far as these depend on the forms and disposition of the structural elements, between—not into—which the vessels penetrate. But the closeness of the network, and the consequent number of the capillary vessels in a given space, are proportional to the activity and importance of those functions.

The capillaries form the intermediate blood channels between the finest arteries and veins. When examined in the transparent part of a living animal, they are seen to be of different sizes, some conveying two or more rows, and others only a single row, of blood corpuscles. Moreover, when watched sufficiently long, they are observed to undergo slow changes in diameter, so that vessels, at one time capable of conveying several rows of blood corpuscles, shrink, and no longer convey more than a single row, or even become temporarily incapable of admitting any corpuscles, so that they merely convey the liquor sanguinis. It was at one time supposed that vessels, named *vasa serosa*, or *serous vessels*, constantly so small as only to admit the fluid portion of the blood, existed in all or many parts of the body; but their presence generally, which was purely conjectural, has not been confirmed. By some authorities, however, it is at least suggested that, in

the cornea, capillaries may exist, which habitually convey only the liquor sanguinis (Kölliker, Hyrtl).

In watching the capillary circulation, it is seen that such vessels as have ceased for a time to convey blood particles, again dilate and admit them, and, from this alternate contraction and dilatation, a vital contractility has been attributed to the coats of these vessels. The structure of their delicate walls, however, which are composed of homogeneous membrane containing nuclei but destitute of muscular fibre-cells, negatives the idea of their possessing a vital contractility; and, moreover, it has been found that no contraction, or other change, of these walls, occurs on the direct application of the electric stimulus to them. Their walls are, however, elastic, and the changes in diameter of the vessels, are probably due, either to disturbed conditions in the neighbouring small arteries, owing to the contraction or relaxation of their muscular coat, or to movements in the tissues in which the capillaries are distributed, and in which organic muscular fibres, fibre-cells, or other contractile elements, such as pigment-cells, are frequently present. The capillaries do not, therefore, seem to exercise any mechanical influence on the circulation of the blood through them, by virtue of an active contractile force, resident in their walls; but they may adapt themselves, by their elasticity, to the varying quantities of blood, distributed to any particular part. Such conditions must occur in the opposite states of blushing and pallor of the skin; in the conditions of fulness or emptiness of the capillaries of a gland or membrane, according as it is secreting or not; and in the condition of health and inflammation, in any vascular part, such as the conjunctiva of the eyeball.

The real propulsive *cause* of the motion of the blood in the capillaries, is the same as that of the arterial circulation, viz. the ventricular systole, modified, in its effects, by the resilience of the elastic coat of the arteries themselves. Indeed, in a living animal, if the force of the left ventricle, communicated to the blood in the arteries, be arrested by pressure on, or ligature of, those vessels, the stream of blood in the capillaries soon almost entirely stagnates, and the venous current beyond them is stopped, whilst the tension or blood pressure in the arteries also ceases. Moreover, in the fish, as we shall hereafter find, the force of the single ventricle of the heart, is sufficient to propel the blood first through the gills, and then through the arteries of the body. It has been supposed that certain mutual attractions and

repulsions between the blood and the tissues lying outside the systemic capillaries, or between the blood and the air in the lungs, may influence the movement of the blood through the capillaries, and even constitute a moving power in the capillary circulation. But this implies an attractive force in regard to the blood in the arterial half of the capillary network, and a repulsive force in regard to the blood in the venous half of that network, an hypothesis complex, and yet unproved.

The supposition of the existence of a local attractive and propulsive force, exerted on the blood passing through the capillaries, is held to be supported by the following facts:—The gradual emptying of the arteries after death; the maintenance of the circulation in the portal system; the periodic and local changes in the circulation during secretion, or in other conditions, such as fainting and fright, or in diseases such as congestion and inflammation; the obstructive changes which occur in the pulmonary circulation during asphyxia; the great activity of this circulation, when the respiratory changes are rapid; and lastly, the fact of a circulation of blood occurring in the embryo of animals before the development of the heart (Draper). It has been further pointed out, that of two fluids contained in a capillary tube, that which has the greatest affinity for the sides of the tube, will flow along it quicker than the other, owing to mere physical action.

On the other hand, it is alleged that, although a healthy condition of the walls of the capillaries and of the tissues beyond them, and a healthy performance of their functions, are necessary to an unimpeded flow of the blood through these vessels, and although a *stasis* or stagnation of the blood, and a dilatation of the capillaries, accompany a state of inflammation, imperfect secretion, or defective respiration; yet such facts do not prove the existence of a special propulsive force, resident in the walls of the healthy capillaries, or dependent upon the healthy nutritive, secernent, or respiratory function; they may merely show that the capillary circulation, though dependent upon the action of the heart and arteries, may be retarded or arrested by abnormal relations between the blood and the tissues, or air, outside the capillary walls. The enlargement of the capillaries, which accompanies such stagnation of the blood in them, and also the shrinking of these vessels, as the part recovers, imply an exercise of elasticity by their walls; but this cannot be, under any circumstances, a moving force in the circulation, but rather a means

of adapting the size of the capillaries, to variations in their contents.

The motion of the blood in the capillaries, when observed under the microscope, in animals not too much disturbed in the experiment, is constant, equable, and regular; but the character of the movement, may be modified by the dilatation or contraction of the neighbouring small arteries under the action of cold or other stimuli, by obstructions in the veins, and by the condition of the heart itself. When, as already mentioned, the heart's systole is weak, the motion of the blood in the capillaries, may, from the non-development of a perfect recoil in the arteries, become pulsatory; and when the heart is still more enfeebled, the blood in the capillaries may merely oscillate, or be completely arrested, or a backward current may even take place in it. These and many similar disturbances, even under the microscope, have been often erroneously referred to active influences in the coats of the capillaries, or in the surrounding tissues.

The motion of the blood in the capillaries, is more rapid in the centre of each little stream, and slower at its surface, near the walls of the vessel. The existence of corpuscles in the living blood, affords the means of determining this fact; for the red corpuscles may be seen to move, comparatively swiftly, along the centre of the vessel, whilst the white corpuscles travel, much more leisurely, along the sides, the ratio of their respective movements being as 9, or even 17, to 1 (Weber). The outer, thin, more slowly moving film, in contact with the inner surface of the capillaries, measures, under different circumstances, from $\frac{1}{5}$ th to only $\frac{1}{8}$ th of the diameter of the vessel. It forms the *still layer* or *space of Poiseuille*, in which the white corpuscles move slowly along, as if some special attraction retained them against the sides of the vessel, whilst the red corpuscles are hurried along the centre. This striking phenomenon may have, in part, a physical explanation; for a retardation always occurs in the movement of that portion of a fluid which is in contact with the walls of a tube, as compared with the rate of motion along its axis, this effect being due to friction in large tubes, and also to capillary attraction in small tubes. In the living animal economy, the retardation of the circumferential layer of blood in the capillaries, must have an important influence on the nutritive, secretive, and respiratory processes, all of which are accomplished within a certain range of the capillary circulation; it may merely

facilitate the withdrawal from the blood, and the escape through the capillary walls, of certain necessary materials; or it may be itself an indication of nutritive, or other, attractions from without, operating on the stratum of fluid lying next to the thin capillary walls. Some such attraction may prevail between the pale corpuscles and the walls of the vessels themselves, but the existence of this has not been established. These corpuscles, however, appear to be naturally much more adhesive than the red corpuscles, as is shown by their clinging to a glass slide or cover, as seen when a minute drop of blood is spread out and examined under the microscope.

The actual rate of motion of the blood in the capillaries, as watched and measured by aid of the micrometer in the field of the microscope, in the case of individual blood particles, has been found by various observers to be, in the frog's web, rather more than 1 inch per minute, in other words, about $\frac{1}{60}$ th of an inch per second (Hales, Valentin, Weber). As to the warm-blooded animals, the rate of motion is higher, being, according to Volkmann, 1·8 inches per minute in the dog; whilst the observations of Ludwig and Vierordt on the entoptical retinal image, or image of Purkinje, give a velocity, in the retinal capillaries of their own eyes, of from about $1\frac{1}{5}$ th inch to rather more than $1\frac{3}{4}$ inch per minute. The average velocity in Man, might therefore fairly be estimated at about 2 inches per minute, or $\frac{1}{30}$ th of an inch per second, *i.e.* twice the velocity in the frog. The apparent rate of motion of the blood, in the capillaries of either a warm or cold-blooded animal, as seen under the microscope, is so high, that the observer is apt to be misled with regard to its actual velocity; and, deceived by the apparent motion, to doubt that the real velocity is only 1 inch per minute in the cold-blooded animal, and 2 inches per minute in the warm-blooded animal. But the area of observation being enormously magnified, the apparent or angular motion of the blood before the eye of the observer, is increased in the same proportion; so that in the field of a microscope magnifying 180 diameters, the rate of motion of the capillary blood, *appears* to be, in the frog, 180 inches per minute, or 3 inches per second, and in the warm-blooded animal, to equal twice that velocity. The actual slow rate of motion of the blood through the capillaries, is remarkable and important, in connection with the nutritive, secernent, and respiratory functions, giving ample time, as it were, for the important interchanges between the blood and the tissues

or the air, which take place in them, especially for those of deoxygenation and oxygenation, which occur, the former in the systemic, the latter in the pulmonary, capillaries.

The slow rate of motion of the blood in the capillaries, is even more striking, when it is compared with the rate of motion in the arteries, which, as already mentioned, is estimated at about 10 inches per second, or 600 inches per minute, in the human carotid, so that the velocity of the blood in the systemic arteries, is 300 times greater than that in the systemic capillaries. It has been calculated that in the pulmonary capillaries, the rate of motion of the blood is five times greater than the average rate in the systemic capillaries, *i.e.*, 10 inches per minute, or the $\frac{1}{6}$ th of an inch per second.

This remarkable retardation of the blood in the capillary vessels, as compared with its velocity in the arteries, is doubtless, in part due to increased friction, dependent on the vast increase in the number of channels through which the blood now has to pass; but its chief cause is the very great increase in the *capacity* of the capillary, as compared with that of the arterial system. It has already been stated that the combined sectional areas of the first and second degrees of arterial branches, as a rule, slightly exceed the sectional area of their common trunk. In the smallest arteries this is doubtless much more marked; and on arriving at the capillaries, the increase in the total sectional area of the bloodvessels, or, as it is otherwise expressed, in the capacity of the capillary system, is sudden and immense. A fluid moving from a small into a wider tube or channel, has its motion retarded accordingly; and the change of capacity, in passing from the arterial to the capillary system, has been compared to that which would take place in a very short cone. The relative areas of the two systems of vessels, are usually, indeed, estimated, as bearing an inverse ratio to the measured velocity of the blood in them. Hence, according to the preceding data, the sectional area of all the capillaries in the human body, would be at least 300 times greater than that of the chief arterial trunks. It has also been calculated to be about 400 (Volkmann), 500 (Donders), and even more than 800 times (Vierordt), greater than the area of the aorta.

Motion of the Blood through the Veins.

The position and structure of the veins, and of their valves, have been described in vol. i. pp. 18 and 58. Their walls,

though thinner, and more easily compressible, than those of the arteries, and less elastic and contractile, are very strong, the vena cava having been found to require a greater force to burst it, than the aorta. Collecting the blood from the capillaries by minute venous radicles, the systemic veins convey the dark blood, from all parts of the body, back to the right auricle of the heart. In the limbs, the superficial veins lying beneath the skin are not subjected to the pressure of muscles; whereas the muscles must press upon the sides of the deep veins. The pulmonary veins, which convey bright blood from the lungs to the left auricle, are peculiarly circumstanced, being, like the pulmonary arteries, situated entirely within the chest.

The blood in the veins, as indicated by opening a vein in the living body, moves by an even flow, destitute of any pulsatory or jerking movement; for the rhythmic character of the heart's action, is already lost in the capillaries, and the equable flow of blood in them, necessitates a corresponding equability in the motion of the venous blood. But the primary force which urges on the blood in the veins, is still the heart's action, modified by the resilience of the arteries, which, after having nearly exhausted itself, in propelling the blood through the capillaries, is still adequate to move on the blood in the veins. The chief resistance in the circulation of the blood, takes place in the capillaries, where, doubtless, it is very great; indeed, the force of the blood in the veins, as measured by hæmadynamometers fitted into those vessels, varies from $\frac{1}{10}$ th to $\frac{1}{20}$ th of that of the blood in the corresponding arteries (Poiseuille). In the dog, the blood pressure in the jugular vein, is from $\frac{1}{11}$ th to $\frac{1}{12}$ th of that in the carotid artery (Valentin); but the blood pressure diminishes, in proceeding from the branches to the larger veins, and in the great veins close to the heart, the pressure is scarcely appreciable. But certain facts seem, nevertheless, to show that this force is really the residue of that of the left ventricle, which is therefore an adequate cause, and probably the true cause, of the motion of the blood in the veins, towards the right auricle. First, pressure upon *all* the arteries of a given part, arrests the flow of blood from a wounded vein belonging to the same part. Secondly, if the venous circulation from a given part, be entirely arrested, by pressure on, or ligature of, the veins, the blood-pressure in them is said to rise, so as even to be equal to that in the corresponding arteries (Magendie). Thirdly, as already

stated, when the heart's action is weakened, its rhythmic force is propagated into the capillaries, giving a pulsatory movement to the blood contained in them, and so establishing the fact that the heart's action extends to that part of the circulation; but, besides this, under certain conditions, oscillations occur in the blood-pressure in the veins, as indicated by the hæmadynamometer. Fourthly, water injected into the arteries, with a force less than that of the heart, returns through the veins. Lastly, it has been shown by Dr. Sharpey, that defibrinated ox's blood injected into the thoracic aorta of a dog, passes freely back by the veins of the lower limbs; also, that if the aorta be tied in the abdomen, below the origin of the arteries of the stomach and intestines, the blood still returns along the inferior vena cava. In the former case, the blood passes through a single capillary system, namely, that of the lower limbs, whilst, in the latter, it is propelled through two sets of capillary vessels, viz. through those of the alimentary canal, into the portal venous system, onwards through the capillary plexuses of the hepatic lobules, and then through the hepatic veins into the vena cava inferior. The pressure employed in these experiments, as measured by the hæmadynamometer, was maintained at about 6 inches of mercury, which is known to agree with the force of the left ventricle in the living dog. To propel the blood through the pulmonary arteries, capillaries, and veins, a less force was sufficient. From the preceding considerations and experiments, the adequacy of the heart's force, to complete the circulation of the blood back to itself, may therefore be considered as established. The position of this organ in the centre of the circulatory system, its large muscular mass, and the proportionate thickness of the right and left ventricles to the work which each has to perform, likewise favour the conclusion that the heart, when present, is the real agent in the circulation of the blood. A circulation also takes place, however, in so-called acardiac embryos, in which the heart is absent, though, in some of these, the movement of the blood may depend on the action of the heart of a conjoined embryo. Again, in the early embryo of the chick, a movement of the blood in the so-called vascular area, is noticeable before the heart begins to pulsate; but this movement is irregular, and takes place from the vascular area towards the embryo. Moreover, as we shall hereafter see, a true circulation takes place, in contractile vessels, in certain of the lower animals, which are destitute of

a heart. Lastly, in plants, examples are met with of a circulation independent even of contractile vessels or cells. The advocates of the existence of a force, originating in the capillaries or their neighbourhood, relying on these and other facts already mentioned, of course suppose it to be superadded to that of the heart in the venous circulation.

The motion of the blood in the veins, and its consequent return, through them, to the heart, are *aided*, in Man and the higher animals, by certain secondary or so-called adjuvant causes, such as the pressure of the muscles, and the thoracic respiratory movements.

In a few exceptional cases, the veins themselves possess a power of rhythmic contraction; the veins in the delicate ears of the rabbit, have been seen to pulsate; in the bat's wings, the veins contract from 8 to 10 times in a minute (Wharton Jones). The caudal vein of the eel, the portal veins of the myxine, and some of the abdominal veins of the amphioxus, are also pulsatile at certain points.

The effects of muscular pressure, considered as an aid to the circulation, are entirely due to the presence and direction of the valves in the interior of the veins. These are found chiefly in the veins of the limbs, especially in the superficial veins, and also in the large veins at the root of the neck. Furthermore, the free edges of the valve-segments being turned towards the heart, in the direction of the venous blood-current, the valves allow the return of blood to the heart, but are speedily closed, when any obstacle to the onward flow of the blood occurs, as when a vein is compressed between a valve and the heart. Under such circumstances, the reflux of the blood in the veins, from its trunk to its branches, is checked, and on any additional pressure, the blood contained in the veins, is urged on towards the heart. Moreover, owing to the frequent anastomoses between neighbouring veins, some of the blood may also be pressed into collateral channels, which are not subjected to pressure, and so be aided in its progress to the heart. This is exemplified by the increased quantity of blood forced into the superficial veins of the limbs, during muscular efforts which compress the deep-seated veins. In the actions of different muscles in the various movements of the body, sometimes one set of veins, sometimes another, must be compressed; and the varying degrees of compression to which the deep-seated veins especially are subjected, must assist or hasten the return of blood to the heart. But this is not an essential cause of the venous circulation, for that is perfectly performed during the

most complete rest of the muscles of the limbs, as in the state of repose, sleep, and paralysis ; moreover the circulation through the brain is performed altogether independently of muscular pressure, and of the presence of valves in its veins. When, owing to muscular exertion, a larger quantity of blood is returned to the heart in a given time, the frequency of the heart's beats is always increased, a mutual adaptation being thus evidenced, between the rapidity with which the blood is returned to the heart, and that with which the heart endeavours to transmit it onwards.

The respiratory movements have been long believed to aid in the systemic circulation of the blood. Unlike the pulmonary circulation, the systemic circulation is partly performed within, but partly, and chiefly, without, the thorax ; hence different portions of it, are unequally affected or disturbed by the thoracic movements. It has already been stated that during, and almost to the end of *expiration*, the blood pressure in the systemic arteries is increased ; the effects of this increased pressure have even been recognised beyond the capillaries, in the veins ; for the flow of blood from a divided vein becomes stronger at each expiration. But expiration, though it aids the arterial current, must, when the continuity of the veins is perfect, retard the venous current ; for the chest walls must then compress the contents of that cavity, including the right auricle and great venous trunks, and so hinder or check the flow of blood into them. This is shown by the accumulation of blood in those veins, by the congestion of the face, and by the distension of the veins of the neck and forehead, during expiratory efforts, such as coughing or sneezing, and holding the breath, with or without some other accompanying effort. The expiratory thoracic movements cannot, therefore, be regarded as contributing to the venous circulation, the effect on the blood in the arteries, being more or less counterbalanced by that on the blood in the veins. The *inspiratory* movements increase the arterial blood pressure, without otherwise affecting the blood-current in the arteries ; because the semilunar valves prevent regurgitation towards the thoracic space. But the absence of similar valves at the entrance of the *venæ cavæ* into the right auricle, so far permits the influence of inspiration on the blood in the great veins, as to facilitate its entrance into the thorax, *i. e.* into the great venous trunks and the right auricle of the heart.

If a bent tube be inserted into the jugular vein of an

animal, and its lower end be dipped into fluid, the latter will be found to rise within the tube, at each inspiration, sinking again, even a little below its original level, during expiration (Sir D. Barry). The blood pressure, as measured by the hæmadynamometer, has also been shown to be less, by from 3 to $7\frac{3}{4}$ inches, in the veins during inspiration, especially in those near to the chest; in the sciatic vein, on the other hand, it is no longer observed. If the veins had rigid walls, the effect of inspiration in drawing the venous blood into the thorax, would be considerable; but the collapsible character of their coats, and their yielding on pressure, prevent this exhausting process. At the root of the neck, the great veins are more or less supported by, or attached to, the bones or other parts, and so may be partially maintained in a pervious condition. The effect of inspiration is, indeed, limited to the large veins close to the thorax; for, as we have seen, the blood pressure in the more distant veins of the limbs is not increased during inspiration. It is this suction force towards the chest, during inspiration, which has been named, in regard to its effect on the circulation, the *vis a fronte*, in contradistinction to the *vis a tergo*, derived mainly from the heart, modified by the arteries, possibly aided by the nutritive and respiratory work accomplished through the capillaries, and certainly assisted by muscular pressure. The existence of this suction force towards the thorax, and its influence on the venous blood-current, are illustrated by the accidents which have sometimes occurred in surgical operations in the region of the neck, when air has been drawn in through wounded and patulous veins, and has occasionally caused death. Horses have been often killed by blowing air down the jugular vein. The right side of the heart is, in such cases, found filled with frothy blood. The cause of death is probably due, not to paralysis of the muscular fibres of the heart, but to the mechanical impossibility of the passage of frothy blood through the capillaries of the lungs.

The presence of valves in the veins near the heart, also contributes to the intermittent aid given to the venous circulation by the respiratory movements; for, whilst they permit, during inspiration, the influx of blood through the large veins into the chest, they prevent the reflux of the blood in them during expiration, so that the balance of advantage is in favour of the return of the venous blood. The valves of the jugular veins not only serve this purpose, but also prevent the regurgitation of the blood towards the brain, during coughing, or other

efforts accompanied by violent expiration or compression of the chest. This reflux motion of the blood in the great veins of the neck, is shown by alternating conditions of fulness and emptiness of those vessels, synchronous with expiration and inspiration, producing the so-called *respiratory pulse*. In cases in which portions of the skull have been removed in the living body, and in which the veins within the cranium, protected from atmospheric pressure at their sides, may be compared to the tube in Sir D. Barry's experiment, an alternate rising and sinking of the brain have been observed, corresponding respectively with the movements of expiration and inspiration. These movements must be distinguished from the slighter pulsatory movements coincident with the heart's action, and dependent on the pulse of the cerebral arteries. In constrictive disease of the valved orifices of the heart, the return of blood into that organ from the veins, is impeded, and those vessels, accordingly, become permanently distended near the heart. Such disease almost always affects the orifices on the left side of the heart, and its effect on the great systemic veins, is communicated backwards, indirectly, through the pulmonary circulation. Even in the healthy condition, the imperfect closure of the tricuspid valve causes a venous pulse at each ventricular systole, the shock being conveyed through the blood in the right auricle, and thence into the veins of the neck, as far as the first set of valves.

The effects of *gravity* on the venous circulation, or rather on certain parts of it, have been sometimes erroneously estimated; for it was imagined that the upward current through the veins in the lower part of the body, *i.e.* below the heart, was resisted by the weight of the column of blood below that organ; whilst the venous circulation in the upper half of the body, *i.e.* above the heart, was thought to be aided by the weight of the corresponding column of venous blood. But the circulation of the blood being performed in a *closed* system of vessels, consisting, as it were, half of arteries and half of veins, which meet in the capillaries, the weight of the venous blood in the lower limbs, is counterbalanced by that of the arterial blood. Hence, the gravity of the venous blood does not, *per se*, offer, such an obstacle to the circulation, as requires to be overcome by the force of the heart; for the two columns of blood balance each other hæmostatically, like columns of water in a U-shaped tube. With regard to the vessels above the heart, they also form a double closed system, and the advantage of gravity

on the venous side, is, so far as the heart's action is concerned, counterbalanced by the disadvantage on the arterial side.

Gravity, however, does actually affect the circulation, through its influence on the circulatory organs, especially on the capillaries and veins; for these vessels are not rigid, like a U-shaped tube, but yielding. The weight of the entire column of venous blood, for example, is supported by the coats of the veins, those of the lower limbs having more weight to bear than the veins of the trunk, and these again more than the veins of the upper limbs, neck, and head. Hence the coats of the veins, in the lower limbs, especially those of the less supported subcutaneous veins, are proportionally thicker than those in the upper parts of the body, the coats of the jugular vein being very thin, and those of the saphenous vein very thick, in proportion to their size. Hence, too, the valves are more numerous, and of greater strength, in the veins of the lower limbs than in those of the upper limbs; whilst in the neck, they exist only in the neighbourhood of the chest. The mechanical effect of these valves, is to save the entire length of the vein from the total pressure of the venous column, and to divide it into shorter subordinate columns, into which, however, weight is still transmitted by the collateral veins. When the valves of the veins of the lower limbs, are weakened, and no longer close perfectly, those vessels become distended, and *varicose*. If the tonicity and elasticity of the smaller veins be impaired, or overcome, by prolonged over-distension, from obstructions to the return of blood from them, or by general debility, the fluid part of the blood is liable to escape through the coats of the capillaries and minute veins, so as to cause *dropsy*.

The *rate of motion* of the blood in the veins, is much quicker than that in the capillaries; but not so quick as in the arteries. In the jugular vein of a dog, the rate of motion has been estimated at $6\frac{4}{5}$ th inches per second (Volkmann). Considered generally, the average velocity of the blood in the veins, is said to be from $\frac{1}{2}$ to $\frac{1}{3}$ of that of the blood in the corresponding arteries; this estimate is founded on the supposed relative capacity of the venous, as compared with the arterial, system, which is believed to be as 2 or 3 to 1. As the velocity of the arterial blood diminishes in the smaller arteries, partly in consequence of friction, but also owing to the increased capacity of the branches in comparison with the trunks, so inversely, as the veins diminish in capacity from their

branches to their trunks, the velocity of the blood in them increases as it approaches nearer and nearer to the heart, and, in the larger veins, becomes equal to about $\frac{3}{4}$, or more, of the velocity in the corresponding arteries. The form of the entire vascular system has indeed been likened to two bent cones, joined at their apices in the heart, and at their bases in the capillary system. The quantity of blood received by the right auricle, closely agrees with that thrown from the left ventricle; hence, therefore, the velocity of the venous current, as it enters the right auricle, must be less than that of the arterial blood passing through the aortic orifice; for the combined areas of the two venæ cavæ, are greater than the area of the aorta.

The rate of motion of the blood in the veins, is more subject to *disturbing causes*, whether of acceleration or retardation, than in any other part of the circulation. Thus, the effects of muscular pressure, though, on the whole, favourable to the onward flow of the blood in the veins, are necessarily intermittent, according or not as the muscles are at play. Again, the opposite influences of expiration and inspiration, though felt only within a certain distance of the thorax, and so affecting the rate of motion of the blood in the large veins only, are themselves liable to great variations, according to the activity, violence, or depth of the inspiratory or expiratory movements. Such variations occur constantly during life, and incessantly alter the rate of motion of the venous blood-current. In experiments on animals not subjected to the continued and uniform influence of chloroform, the struggles, and the respiratory efforts of the creature, greatly disturb the velocity of the venous current, sometimes checking, sometimes accelerating, it. Individual estimates of the velocity of the blood in the veins, must therefore be accepted, with some reservation.

There are certain *peculiarities in the venous circulation* of particular parts of the body. Thus, the *portal* circulation is peculiar, from the fact that the blood passes in it, through a second capillary network, before it returns to the heart; for the blood which circulates thus through the liver, has already been driven through the capillary vessels of the other abdominal organs of digestion. There are no valves in the portal or hepatic veins; but the latter are retained constantly in a pervious state, by their adhesion to the substance of the liver, a condition favourable to the passage of the blood from that organ. Again, the circulation within the

cranium, presents peculiarities; the arterial trunks which enter it, four in number, are of large size, traverse bony passages in their way to the cranial cavity, and unite by anastomoses in the interior of the skull, at the base of the brain, all which arrangements are calculated to secure a full and free supply of blood to the brain, under various conditions of external pressure, or other impeding causes. Besides this, the proper arteries of the brain, ramify, in an unusually tortuous manner, upon its complex surface, and at last divide, in the pia-mater, into a close web of numberless branches supported by a delicate cellular tissue; from these, long slender minute vessels enter the brain at all points, ensuring a perfect supply of blood, and its even and gentle entrance into the delicate cerebral substance. The veins within the cranium present special modifications; first, they have no valves; moreover, the largest venous channels consist of passages between layers of the dura-mater, the fibrous membrane which immediately lines the skull; hence, they are not subjected to accidental pressure, such as might interfere with the blood-current within them. Lastly, as the cranium itself has unyielding walls, the circulation of the blood through the brain, is carried on under very peculiar conditions, as compared with that of other organs, which are subject to atmospheric, and perhaps muscular, pressure also. The brain and the blood being incompressible, the quantity of blood within the cranium, must either be always the same, or else some special provision must exist for its increase or diminution in quantity. It has been suggested, that the quantity of blood in the cranium is absolutely unalterable, and that the only changes which can take place in the cerebral circulation, are various compensatory displacements of the blood, in the interior of the arteries, veins, and capillaries; but experiments have shown that the brain of an animal may be rendered pallid, *i.e.* may be deprived of the blood in its vessels, by extreme venesection. Moreover, the presence of the cerebro-spinal fluid (vol. i. p. 295), and the known rapidity with which the secretion and absorption of so diffuent a fluid, may take place, afford a feasible explanation of the mode in which variations in the quantity of blood in the vessels within the cranium, may be rapidly counter-balanced.

The *pulmonary circulation* presents many peculiarities. Its arteries convey dark or deoxygenated, and its veins bright or oxygenated, blood. Neither its veins or arteries anastomose,

except in their very finest ramifications; its veins have no valves, either in their course, or at their entrance into the left auricle; its capillaries are large, most numerous, and very short between the arteries and veins. As every part of the pulmonary circulation is carried on within the thorax, the flow of blood from the right ventricle, through the pulmonary vessels, to the left auricle, is, unlike the systemic circulation, equally influenced in every part, at each moment, by the varying conditions of thoracic pressure. Lastly, the loops of the pulmonary circulation are much shorter than those of the systemic vessels, and the blood takes much less time in passing through them. The velocity of the blood is greater, and the blood pressure much less.

Period of a complete Circulation.

It has been seen that the chief cause of the circulation of the blood in Man, and in animals possessing a heart, is undoubtedly the muscular force of that organ; that the relative velocity of the blood-current in its several parts, is quickest in the arteries, slower in the veins, and slowest, by many degrees, in the capillaries, the actual rate in the large arteries being about 10 inches per second, in the small arteries probably about 2·2 inches per second, in the capillaries about $\frac{1}{30}$ th of an inch per second, and in the medium-sized veins from about $\frac{1}{2}$ to $\frac{1}{3}$ of the rate in the corresponding arteries; and lastly, that the rate of movement through the pulmonary circulation, is five times more rapid than that through the systemic circulation. There remains yet to enquire, in what period of time the complete circulation is performed, that is to say, in what time, a given minute portion of blood, thrown from the left ventricle, or passing any other given point of the circulation, will flow through the body and lungs, back to the same point. The conclusion arrived at on this subject, based on many experiments in animals, is, that, in Man, a complete circulation of a given particle of the blood, may be performed within a much less time than one minute. A solution of ferrocyanide of potassium (selected for the facility with which it may be detected by appropriate chemical tests), being injected into the right jugular vein of a horse, successive portions of blood are drawn from the opposite jugular vein, and subsequently tested; the presence of the salt has been detected in the portion of blood so drawn, at the expiration of 30 or even of 20

seconds (Hering). In such an experiment, the ferrocyanide of potassium could not have passed through the tissues across the neck, from one vein to the other, but must have proceeded with the blood along the right jugular vein, to the right side of the heart, thence, through the pulmonary vessels, to the left side of that organ, next through the aorta, carotid arteries, and capillaries of the head and neck, and thence along the veins into the left jugular; in other words, it must have performed, with the blood, a complete circuit through the lesser circulation in the lungs, and through that part of the greater circulation which belongs to the head and neck. The passage of the ferrocyanide of potassium, from the jugular vein, through the lungs, and thence, through the hinder limbs of the horse, to the great saphenous vein of the thigh, takes place in 20 seconds; and, from the same vein, to various arteries of the body, in still shorter times, viz. to one of the facial arteries in 10 seconds, but to more distant arteries, as *e.g.* to the metatarsal in the hind limb, in from 20 to 40 seconds (Hering).

Similar experiments have been made, but on an improved method, by arranging a series of small cups on a rotating apparatus, so that they can be quickly moved in succession, before an aperture in a vein; in this way, the blood is collected at very short and exact intervals. The time occupied in a complete circulation of the blood, can thus be determined even in small animals. In them, speaking generally, the passage of poisonous substances injected into the veins, takes place more quickly than in the horse. In the dog, the time is found to be 16·7 seconds; in the rabbit, nearly 7·79 seconds; in the cat, 6·69 seconds, and in the squirrel, 4·39 seconds; in the horse, it is 31·5 seconds (Vierordt). Allowing for the obvious effect of size, and consequent length of the bloodvessels, it must be concluded that the blood in the human body, performs the complete round of the circulation, in even less than half a minute.

Vierordt has pointed out a remarkable relation between the frequency of the pulse, that is, of the heart's beats, in different Mammalia and Birds, and the ascertained average period of the complete circulation in them. The frequency of the pulse in these animals, increases, generally, as their size diminishes, being, for example, in the horse, dog, cat, rabbit, and squirrel, respectively, 55, 96, 240, 220, and 320 in the minute, or 60 seconds. But, as we have seen, the times of a complete circulation in them are, 31·5, 16·7, 6·69, 7·79, and 4·39 seconds. From such data, it is shown, that a complete circulation, in these several animals, is

performed during the following numbers of heart's beats; viz. 28·8, 26·7, 26·8, 28·5, 23·7. Thus, in the horse, for example, as 60 sec. : 55 beats :: 31·5 sec. : 28·8 beats. In the larger Birds, nearly the same proportion prevails; and the mean relation is found to be about 27 heart's beats for each complete circulation.

In Man, Vierordt calculates that, with the pulse at 72 per minute, the heart's beats are 27·7 for each complete circulation, which is accordingly performed in 23·1 seconds, or less than half a minute. Thus as 72 : 60 :: 27·7 : 23·1.

Every portion of the blood does not complete its circulation in exactly the same time. As regards the pulmonary circulation, but little difference can occur, whether a given portion of blood passes through the right or the left lung, or through this or that portion of either lung, on its way from the right to the left cavities of the heart; but even here, certain differences in the length of the route pursued by different portions of blood, must exist. In the systemic circulation, however, the differences are much more marked; the shortest route through which a portion of the blood has to pass from the left to the right cavities of the heart, is that through the nutrient vessels of the heart itself, and the longest route, that through the vessels of the lower limbs. Different portions of the blood have, indeed, to circulate through arches of varying length, and hence the time which they take to traverse different parts of the body, must be somewhat different.

The slow rate of motion of the blood through the capillaries, only 2 inches per minute in warm-blooded animals, appears, at first sight, to be opposed to the above-mentioned conclusion as regards the high rate of velocity of a complete circulation; for in that circulation, the blood passes through two sets of capillary vessels, pulmonary and systemic, besides traversing the arteries and veins of those two circulations, as well as both sides of the heart. But it has been estimated that the systemic capillaries of any given organ or tissue of the body, numberless as they are, cannot measure, from the finest arteries to the finest veins, more than about $\frac{1}{10}$ th of an inch in length; the pulmonary capillaries must be still shorter. According to Vierordt, the systemic capillaries do not measure, on an average, more than $\frac{1}{50}$ th of an inch in length, although these limits are not well defined. The blood may therefore pass through both the systemic and pulmonary capillaries, in a period of about $3\frac{1}{2}$ seconds only (viz. in 3 seconds through the former, and in $\frac{1}{2}$ a second through the latter-named vessels). Assuming

with Vierordt, the total period of a circulation at about 28 seconds, in a man of average height, this would leave a balance of $24\frac{1}{2}$ seconds for the passage of the blood through the arterial and venous channels and the heart. Supposing the mean length of the arteries and veins to be, in a man of average stature, 30 inches, and the average velocity of the blood in the arteries to be 6 inches per second (the extremes being 10 and $2\frac{1}{4}$ inches), the time required for the passage of the blood through the arteries, would be 5 seconds, and through the corresponding veins, the velocity in which is estimated as being $\frac{1}{2}$ to $\frac{1}{3}$ rd that of the arteries, the time would be $12\frac{1}{2}$ seconds, making in all $17\frac{1}{2}$ seconds, for the circulation through the systemic arteries and veins. To this must be added a period of $3\frac{1}{2}$ seconds, for the passage of the blood through the pulmonary arteries and veins (the rate of motion in them being said to be five times more rapid than in the systemic arteries and veins), making a total of 21 seconds. This, with the $3\frac{1}{2}$ seconds above mentioned as required for the pulmonary and systemic capillary circulations, equals $24\frac{1}{2}$ seconds, or rather more than the 23.1 seconds allowed for the complete circulation. These numbers, though only approximating to the truth, still show that the slow rate of the blood in the capillary portion of the circulation, or in the area of nutritive and respiratory interchanges, is quite consistent with the ascertained rapidity of the circulation, considered as a whole.

The circulation of the blood is said to be generally, but not always, accelerated by an increased frequency of the heart's action. As life advances, it becomes slower.

Quantity of Blood in the Body.

The total *quantity* of blood in the body, has been the subject of much investigation and discussion. The estimates of the older authors, for the most part, were too high, whilst some of those of later writers, probably err in the opposite direction. The actual quantity, in a man of average height and weight, has been supposed, by some, to be 26 or 30 lbs., and by others only 12 lbs. The ratio between the weight of the blood and the weight of the body, the blood included, has been estimated, by some authors, as 1 to $4\frac{1}{2}$, and, by others, as 1 to 13; according to these proportions, which differ so widely, the total quantity of blood in the body of a man weighing 150 lbs., would be either upwards of 33 lbs., or only about $11\frac{1}{2}$ lbs.

Observations on the quantity of blood lost in hæmorrhages, are not considered trustworthy, since in slow bleedings, large quantities of fluid are absorbed from the tissues, to refill the emptying vessels, and so add largely to the amount of blood that may be drawn. The quantity of blood escaping from the vessels in decapitated criminals, added to that which may be subsequently expelled from the vessels, by cautious injections of water, gives a more accurate result. But careful experiments on animals, are of most value. The method of Herbst, which consists in quick bleeding from many vessels opened simultaneously, gives the proportionate weight of the blood to that of the body, as from 1 to 12 in the ox, 1 to 16 in the dog, and 1 to 24 in the rabbit; hence, it would appear that the larger the animal, the greater is the proportion of blood to the body. Valentin compared the specific gravity of the blood drawn from a living animal, before, and after, the injection into its blood-vessels of a given weight of water, the diminution of the specific gravity of the blood, by that quantity of water, serving as a factor in the calculation; this method gives about 1 to $4\frac{1}{2}$ as the ratio to the body in the dog. Chemical substances easy of detection, having been injected into the blood, in known amounts, and the quantity, in a certain portion of the blood drawn from the vessels, having been determined, data have been obtained for calculating the total quantity of the blood; this method shows a ratio of 1 to 8 or 9 (Blake). Welcker's *chromatic* method is so called, because he estimates the amount of blood left in the body after bleeding, by means of the colouring matter. A set of *standard coloured solutions* is first prepared, by mixing a certain known quantity of the blood of an animal, with different known quantities of water. The creature is then bled rapidly to death, and the blood so drawn is weighed. The residual blood in the vessels, is then estimated in the following manner:—the vessels are washed out with free injections of water; the whole body of the animal is likewise divided into small pieces, and macerated, so as to extract all the cruorin in it; these aqueous solutions are then mixed together, and measured, and the tint of the mixture is compared with the standard solutions, and thus the quantity of blood in it is determined. In this way, the proportion of blood to the body, in the dog, is estimated at about 1 to 12.

The quantity of blood in the body, has been calculated by Vierordt, by multiplying the quantity supposed to be expelled from the left ventricle at each systole, by the number of times

the heart contracts during a complete circulation of the blood through the system. The mode in which the latter datum is obtained, has already been explained (p. 258-9); the former is thus arrived at. The average velocity of the blood in the human carotid artery, is assumed to be equal to that in the carotid of a dog, and the sectional area of the vessel being known, it is easy to determine, by multiplying one into the other, the quantity of blood which passes through any part of that artery in a second. Thus 261 millimetres, the velocity of the current in the carotid per second, \times .63 square centimetres, the sectional area of that vessel, $=$ 16.4 cubic centimetres, the quantity which passes through a certain part of the vessel in one second. The quantities passing per second, in the innominate, left subclavian, arch of the aorta, and coronary arteries of the heart, are then estimated in the same way, the rate of motion of the blood in the aorta being assumed to be $\frac{1}{4}$ th faster than it is in the carotid. By these steps, Vierordt arrives at the conclusion that the quantity of blood projected through the orifice of the aorta from the left ventricle, every second, is 207 cubic centimetres, or 219 grammes in weight, or nearly $7\frac{3}{4}$ oz. av. But as the heart beats 72 times in a minute or 60 seconds, there occur $1\frac{1}{5}$ th systoles in each second of time; hence, the quantity of blood thrown into the aorta at each systole, is about 180 grammes, or rather more than 6.3 oz. (p. 213).

As all the blood in the body, must pass once through the aorta, in every complete circulation of that fluid, and as this requires 27.7 systoles to accomplish it, the quantity thrown at each systole, or 180 grammes, \times 27.7, the number of heart's beats, gives, for the total quantity of blood in the body, 4,986, or, in round numbers, 5,000 grammes, which are equal to about 11 lbs. av.; this, compared with the average weight of the body, taken by Vierordt at 140 lbs., is about as 1 to 12.6. The proportion finally adopted by Vierordt, as prevailing throughout the warm-blooded Vertebrata, is 1 to 13. Assuming the average weight of the adult male to be 150 lbs., the usual estimate of English writers, the total quantity of blood in the body, would be about $11\frac{1}{2}$ lbs. av. It has been found that on bleeding an animal soon after feeding, nearly double the quantity of blood is obtained, as compared with the result of bleeding a similarly sized animal in a state of fasting. This circumstance may partly explain the great differences in the estimates above recorded; it also justifies the conclusion

that, in certain conditions of the body, the quantity of blood in the human adult of average weight, may be even as much as 14 lbs.

The quantity of blood thrown into the aorta at each systole, which is likewise the measure of the capacity of the left ventricle, is equal to about $\frac{1}{350}$ th part of the weight of the body. It would further seem that, in warm-blooded animals generally, the quantity of blood flowing through an *equal weight* of the body in a given time, is proportional to the frequency of the heart's beats. Thus, in 60 seconds, the quantities of blood which pass through 1,000 parts in weight of the body, in the horse, in Man, in the dog, rabbit, and squirrel, are, respectively, 152, 207, 272, 620, and 892 parts, the frequency of the pulse in them being 55, 72, 96, 220, and 320. The ratios, accordingly, are all about as 3 to 1. The more rapid the heart's action, therefore, the quicker must be the nutritive changes in the tissues of the body; moreover, as there is no evidence of the capillaries being relatively more numerous in the smaller and quick-pulsed animals, the circulation through their vessels must be relatively quicker,

The Uses of the Blood and of its Circulation.

The blood itself is a highly complex fluid, renewed from, though not altogether formed out of, the lymph and chyle, and perfected, as we shall hereafter see, by the aid of the vascular glands and the respiratory organs. One of its offices is evidently that of providing an exceedingly elaborate material for the nutrition of every part of the body, and for the production of the various secretions which are used in the organism. The fluid character of the blood, fits it for transmission through a vascular or circulatory apparatus, even through the finest vessels; and in this circulation through the body, by means of such an apparatus, its proper nutrient materials are conveyed to all the organs and tissues of the frame, into which a fluid plasma passes through the coats of the capillaries. But, secondly, besides furnishing a constant stream of nutrient material, the blood receives, by absorption into its own current, refuse and effete matters from the whole system, and subsequently transports them to proper excreting organs, by which they are thrown out of the body. Lastly, the dark venous blood receives, through the respiratory organs, a quantity of oxygen from the air inhaled into the lungs, and

transports this oxygen in the red and arterial blood, to every part of the frame, either for its special stimulation, or for combination with its proximate chemical constituents, in the exercise of the functions of those parts; the returning venous blood brings back, amongst other oxidised materials, carbonic acid, and conveys this to its proper excreting apparatus, the lungs, whence it is thrown off. The circulating organs in animals are, therefore, modified, in accordance with the characters of their respiratory organs.

ORGANS AND FUNCTION OF CIRCULATION IN ANIMALS.

Vertebrata.—The *Vertebrata* generally, like Man, have not only a perfectly formed blood, containing coloured and colourless corpuscles, but they also possess a central heart placed in a pericardium, and connected with a completely closed system of bloodvessels, consisting of arteries, capillaries, and veins. In the *Amphioxus* alone, there are no coloured corpuscles, and the heart has no pericardium. As we have seen, the *Vertebrata* only, have a system of absorbent vessels, which empty themselves into the bloodvessels. The size of the red corpuscles in several animals is given in a Table at p. 77–8, vol. i.

But important peculiarities exist in the vascular systems of some of the *Vertebrata*, dependent upon the structure of their respiratory organs. Thus, in *Mammalia*, *Birds*, *Reptiles*, and *Amphibia*, respiration is performed by means of lungs, and hence they are called *pulmonated* or *air-breathing* *Vertebrata*. These consist of two divisions, one including *Mammalia* and *Birds*, in which the temperature of the blood is high, and another, including *Reptiles* and the perfect *Amphibia*, in which the temperature of the blood is low; the former are the *warm-blooded*, *pulmonated* or *air-breathing*, *Vertebrata*, and the latter, the *cold-blooded*, *pulmonated* *Vertebrata*. Again, *Fishes* breathe by means of gills or branchiæ, and constitute the *branchiated* or *water-breathing* *Vertebrata*; they are still more decidedly cold-blooded. In each of these divisions, special modifications of the circulatory apparatus are met with, dependent on differences in the degree, or kind, of their respiration. The Class *Amphibia*, contains animals which commence life as aquatic branchiated creatures, but which, in the adult state, become pulmonated; their circulatory organs are accordingly modified during life, and in a few, which retain, in the adult condition, both gills and lungs, the organs of circulation present a composite form. In all cases, a *portal* circulation is present.

In the *warm-blooded*, *pulmonated* *Vertebrata*, which include the *Mammalia* and *Birds*, the heart, as in Man, consists of four cavities, two auricles, and two ventricles, a right auricle and ventricle constituting the right side, and a left auricle and ventricle forming the left side, of the heart, the two sides being separated by a perfect intervening septum. The general distribution of the vessels is also the same. All the blood which returns from the body to the right auricle, is sent through the lungs, by the right ventricle, and on into the left auricle, before it is

again distributed to the body by the left ventricle. As in the human body, there is a perfect *double* circulation.

Certain minor peculiarities are met with. Thus, the position of the *heart* is usually median, except in the orang-outang, and perhaps in other Anthropoid apes, in which it inclines to the left side, as in Man. In many Ruminants, a bony structure, the bone of the heart, strengthens the base of the ventricular septum. In the dugong, the apex of the heart is deeply notched, the ventricles being there separate; in the manatee, it is less notched.

In Man, and the higher Mammalia, the chief *arteries* spring from the arch of the aorta, unsymmetrically—an arrangement said to favour the distribution of blood to the right fore limbs, rather than to the left; but in the lower Mammalia, the branches arise symmetrically. In the hind part of the tail of the whale, the caudal artery runs, for purposes of protection, through the base of the echelon bones, on the under side of the vertebræ. In many climbing lemurs, in the lion, and other large Carnivora, the brachial artery of the arm passes through an opening in the humerus, and thus is protected from muscular pressure: so also does the artery of the coffin bone, or hoof bone, in the horse.

A cluster of closely ramified arterial vessels, which frequently anastomose together, and again coalesce into a single trunk, is named a *rete mirabile*. Examples of such *retia mirabilia* occur in the carotid arteries within the cranium of the Ruminants, the effect of which may be to check the too rapid flow of blood to the brain, during grazing. Similar structures are found in the fore limbs of the climbing sloths, and lemurs. In diving animals, such as the Cetacea, large *retia mirabilia* exist in the thorax, the object of which is probably to allow the prolonged suspension of respiration during the submergence of those animals.

In the higher Mammalia, as in Man, there is but one superior vena cava; but in the Pachydermata and Rodentia, there are two superior venæ cavæ, and sometimes a cross branch between them, in the neck. Suppose an enlargement of this cross branch, so as to form a left innominate vein, the blood from the left side of the head and neck and the left upper limb, would pass over to the right side, whilst the trunk of the left vena cava might then be obliterated, as far as the heart. In certain diving Mammalia, *venous plexuses*, or *venous retia mirabilia*, exist, in which the impure blood is for a time retained. The portal system, in the Mammalia, is entirely unconnected with the renal veins: sometimes the portal veins have valves.

In *Birds*, the heart is very strong, and lies exactly in the middle line; moreover, the chief branches from the arch of the aorta, are also symmetrical, in accordance with the equal bilateral development, so important and typical in Birds. The veins in Birds, have relatively fewer valves; the portal system communicates, by a few branches, with the renal veins; moreover, the veins of the pelvis and lower limbs, likewise contribute branches to it.

In the *cold-blooded, pulmonated Vertebrata*, which comprise the Reptiles, and the perfect Amphibia, the heart is reduced to three cavities; viz. two auricles and one ventricle. One auricle, the right and larger one, receives blood from the system; the other, the left, usually smaller, receives blood from the lungs; both discharge their contents into the common ventricle, which thus receives a mixture of dark venous blood

from the system, and bright arterial blood from the lungs. From the single ventricle, there proceed, in the Reptilia, a distinct aortic and pulmonary trunk, but in the Amphibia, only a single arterial trunk exists, from which the pulmonary arteries take their origin; in either case, a part of the mixed ventricular blood again passes through the lungs, whilst most of it is propelled through the body. The blood is no longer *entirely* sent through the lungs, before it is distributed to the body again, as happens in the warm-blooded Birds and Mammals, which possess a perfect double circulation; on the contrary, a more or less mixed blood goes to the lungs, and a more or less mixed blood to the body. The pulmonary and systemic circulations are not wholly distinct, but meet in the common ventricle; the circulation is not completely double. In the highest Reptiles, the Saurians, which approach the Birds in so many parts of their organisation, there exists, however, a partial ventricular septum, which, in the crocodiles, is said sometimes to be even complete. The outwardly single ventricle always gives off two arterial trunks, and the internal septum is so placed, that it serves to direct the dark systemic venous blood entering from the right auricle, chiefly into the pulmonary arterial trunk, whilst it turns the current of red arterialised blood coming through the left auricle from the lungs, towards the aortic or systemic arterial trunk. In these animals, then, the circulation approaches closely to the character of the double circulation in Birds and Mammals; but the imperfect structure of the ventricular septum may permit a certain amount of intermixture of the two kinds of blood in that cavity. The right or anterior portion of the ventricle, which is connected with the pulmonary artery, has thinner walls than the left or posterior portion, which is connected with the aorta. In the Chelonia and Ophidia, a less perfect septum also exists, but it gradually becomes smaller, and therefore less able to separate the two currents of blood, or to guide these in special directions. In the perfect adult Amphibia, the single ventricle has either only slight traces of a septum, or, more commonly, no septum whatever; the single arterial trunk, proceeding from it, is sometimes named the *arterial bulb*, or *bulbus arteriosus*. Even the *auricular* septum is imperfect in the Proteus.

The arrangement of the branches of the aorta, in these cold-blooded pulmonated Vertebrata, is also peculiar. In Man and Mammalia, the single aortic arch bends over the root of the left lung, and continues on as the abdominal aorta. In Birds, the arch of the aorta turns down over the root of the right lung, to become the abdominal aorta. In the higher Reptiles, two aortic arches exist, one on each side, forming a right and left aortic arch, which descend over the roots of the corresponding lungs, and join together, somewhere in front of the vertebral column, to form the abdominal aorta. Of these, the right aortic arch, the only one present in Birds, is larger than the left, and evidently forms the proper systemic artery; for it gives off the arteries to the head, neck, and upper limbs, which parts accordingly receive almost entirely red blood, which is directed into the aorta, as already mentioned, by the ventricular septum. On the other hand, the left aortic arch is small, is joined by a short trunk to the pulmonary artery, which springs from the other side of the septum, and from it receives dark blood; hence it follows that the abdominal aorta, formed by the coalescence of the right and left aortic arches, carries mixed blood to the posterior part of the trunk, and the hind limbs.

In the lower Reptiles, three aortic arches exist on each side; the upper pair give off the vessels of the head and neck, the lower pair give origin to the pulmonary arteries, and all combine, by short branches, into two descending trunks, which unite to form the abdominal aorta. Here, also, a more perfectly oxygenated blood is provided for the anterior, or more important part of the animal, a less perfectly oxygenated blood, for the hinder part.

A portal circulation exists in both Reptiles and Amphibia; it is connected with the renal veins, which also exhibit a renal portal system; *i.e.* a set of veins, which convey blood into the kidneys for distribution in their interior. The condition of the organs of circulation in the young or immature Amphibia, will be best understood after that of Fishes has been described.

The *cold-blooded, branchiated Vertebrata*, or Fishes, have no lungs; those organs being represented, however, in a few species, by the so-called *air-bladder*, an appendage, usually, of the pharyngeal part of the alimentary canal. The heart is now simplified by the suppression of the left auricle, there being no pulmonary veins to end in it; the ventricle also is single, as in the Amphibia and Reptiles, but it never presents any trace of an internal septum. There remain, therefore, but a single auricle and a single ventricle. The auricle, like the right auricle in other cases, receives the dark venous blood from the body, and transmits it, through an orifice provided with valves, into the ventricle. This is very muscular, and propels the blood, not into the lungs, for there are none, nor directly into a systemic arterial trunk, or aorta, for immediate distribution through the body generally; but, on the contrary, the single ventricle sends it into a short trunk, called the *arterial bulb*, which has valves at its root, and, in a few examples, is even partially divided into two. From this bulb, a series of arched vessels, usually five, sometimes four, in number, proceed upwards, supported on the cartilaginous branchial arches, and convey the blood, through the branchial arteries, into the gills, in which it passes through capillary vessels, and is then collected by the branchial veins; these running towards the vertebral column, unite together on the dorsal aspect of the alimentary canal, to form a single systemic arterial trunk, which corresponds, in function, with the aorta of the higher Vertebrata. From this, branches are given off to all parts of the body, excepting the gills and generally, if not always, certain parts of the head, which are, singularly enough, supplied by special branches proceeding at once from the branchial veins. From the body generally, the blood is brought back, by the systemic veins, to the single auricle. In the Fish, therefore, all the blood which returns from the body to the heart, is sent first through the respiratory or oxygenating organs, before it re-enters the system; the respiratory apparatus is so interposed that it forms a part of the general circulation, the branchial circulation being continued on to the systemic circulation, without the blood coming back to the heart between them. Hence the circulation in the branchiated Fish, is said to be *single*, as distinguished from the *imperfectly double* circulation of the cold-blooded, and the *completely double* circulation of the warm-blooded, pulmonated Vertebrata. The heart of the Fish, is also said to be a *branchial* and not a *systemic* heart, because its immediate work is to force the blood into the branchiæ or gills. No special contractile apparatus exists beyond the gills, to accomplish the

circulation through the body—a fact which has already been adduced (p. 243), to show that the heart's action is adequate to drive the blood through the systemic circulation of Man, and the pulmonated Mammalia. In the caudal veins of the eel, however, as already mentioned, there exists a pulsating portion, named a *venous heart*, which undoubtedly assists in the return of the venous blood to the distant *proper* heart. Its presence may be connected with the unusual length of the systemic vessels in this part of the eel; but even here, the heart propels the blood through the vessels of the gills, and afterwards through the systemic arteries and capillaries. Pulsating dilatations are likewise found in the arteries of the pectoral fins of the torpedo and chimæra, and in the portal vein of the myxine.

In Fishes, as in other Vertebrata, a portal system of veins exists; it is composed not only of the veins from the digestive organs, but also of those from the other viscera in the posterior part of the abdomen, and likewise of some of those from the hinder part of the body. The venous trunks thus formed, conduct blood to the kidneys as well as to the liver, so that, in Fishes, both these glands receive venous blood. After being distributed through them, the blood is returned to the heart, by proper hepatic and renal veins, which open into the vena cava inferior. Retia mirabilia, both arterial and venous, exist in certain Fishes, on the swimming bladder, in the eyes, and in the neighbourhood of the gills and the intestines.

Since all the blood of Fishes, after its return from the body, passes through the respiratory organs, before it again proceeds to the body, it might be inferred that the respiration must be more complete in them than in the Reptiles, in which only a portion of the venous blood is transmitted to the respiratory organs, whilst some is distributed to the body again. But in Fishes, the respiratory process itself is less active than it is in Reptiles, being aquatic, instead of aerial. As the heart in the Fish, is a branchial or respiratory heart, its single auricle and ventricle have been supposed to be homologous with the right auricle and ventricle, or respiratory heart, of the Bird and Mammal. This view, however, is only partially correct; for though the auricle in the Fish's heart, is homologous with the right auricle of the more perfectly formed Mammalian or Avian heart, and therefore respiratory, the single ventricle represents both ventricles of the heart of the warm-blooded Vertebrata, and, indeed, rather the left than the right ventricle. In the Fish, the branchial vessels given off from the arches, which proceed from the bulbus arteriosus, end in the systemic arterial trunk, and the branchiæ and their vessels, may therefore be regarded as organs interposed in the systemic circulation. In the pulmonated Vertebrata, on the contrary, the pulmonary arteries enter the lungs, from which the blood is returned through pulmonary veins, and these latter do not unite to form an artery, but re-enter the auricular portion of the heart; so that the pulmonary system is not, like the branchial system, continuous with, or a portion of, the systemic, but altogether a special circulation.

The Amphibia begin life as aquatic branchiated animals, but most of them, in their mature state, lose their gills and acquire lungs, so as to become pulmonated, and air-breathing. In this metamorphosis, not only transitions occur in the respiratory organs from the Piscine to the Reptilian condition, but also simultaneous adaptations of the circulating

system. The differences in the mode of respiration, and in the character of the circulation, which are observed between two great Classes of the Vertebrata, viz. Fishes and Reptiles, are exactly paralleled by the differences met with in the immature and mature respiratory and circulatory organs, in an individual Amphibian; and the progressive steps which lead from one state to the other, can be seen in the evolution of a single animal. These changes may be traced in the frog, or in the salamander. In the tadpole of the former, *external branched gills* first appear, but soon become absorbed, and are succeeded by *internal laminated gills*, resembling those of the Fish. In this condition, the heart, composed of a single auricle and ventricle, receives the blood from the body, and propels it into a bulbus arteriosus, and thence, by three lateral symmetrical branches, or *branchial arterial arches*, into the gills; after passing through capillary vessels, it is collected by the branchial veins, from the foremost of which the arteries of the head are given off; these veins, but chiefly the second and third, combine to form the systemic artery or descending aorta, which conveys the blood into the rest of the body, whence it is again returned by the veins, to the single auricle. This form of circulation is truly Fish-like; but at the base of each branchial lamina, a minute vessel runs directly from each branchial arterial arch, to the commencement of the descending aorta; as development goes on, more blood passes through these communicating vessels, directly from the bulb into the descending aorta, without traversing the vessels of the gills; still later, the gills themselves diminish, and more and more blood passes through these little arched vessels at their base; finally, the gills and their vessels, being the one atrophied, and the other obliterated, the whole of the blood proceeding from the ventricle through the arterial bulb, traverses these enlarged symmetrical communicating vascular arches, and so reaches the descending aorta. In the meantime, from the lowermost vascular arch, on each side, there has been developed a little vessel, which ramifies on the walls of a small sac, or rudimentary lung; and as these organs are gradually enlarged, the vessels in question grow, and form the pulmonary arteries. By these, one portion of the blood from the single ventricle, is carried to the newly evolved respiratory organs, the air-breathing lungs; whilst the rest is conveyed through the remaining vascular arches, now reduced to two in number on each side, partly into the arteries of the head and neck, but chiefly into the aorta, and the body generally. Lastly, the blood returning from the lungs, enters a small superadded auricle, or left auricle, which becomes parted off from the right; whilst the blood which returns from the body, enters the ordinary right auricle. Thus is established an incomplete double circulation, precisely the form met with in the lower Reptiles. In passing to the higher Reptiles, the essential change consists in the gradual rising up of a septum within the single ventricular cavity, by which it becomes more and more completely divided into two chambers, as seen in the Saurians, and especially in the crocodile. This change, when quite complete, and constant, produces the perfectly divided ventricles, with their entirely separate pulmonary and systemic arterial trunks, as found in the heart of the Bird and Mammal. Thus are formed the four-chambered heart and the completely double circulation.

Similar changes, in the heart and great vessels, occur in the young

newt or water salamander ; but the external gills not being transitory, or giving place to internal gills, as in the tadpole of the frog, remain throughout the larval condition, becoming, at one time, very large and plumose. Like the internal gills of the tadpole, they receive vessels from the bulbus arteriosus, and, as in them, their disappearance is associated with the same changes in the future distribution of the blood, which is henceforth sent partly to the lungs, but chiefly to the body.

Certain of the Amphibia possess, in their mature condition, both kinds of respiratory organs, viz. external gills and lungs, and are hence named *Perenni-branchiata*. In these, as in the *Proteus*, the condition of the circulation corresponds with that found in the intermediate stages of the larval condition of the newt. Three anterior arches from the bulb, supply the branchial arteries, and a fourth gives a vessel, which becomes the pulmonary artery of its own side ; the pulmonary veins end in a rudimentary left auricle, and the systemic veins in a right auricle ; the ventricle is single, and gives off the bulbus arteriosus, from which arise the vascular arches just mentioned.

In the somewhat anomalous Fish, the *Lepidosiren*, or mud-fish of the Gambia, a remarkable approximation is shown towards the perenni-branchiate amphibian form of respiration and circulation. It has six pairs of branchial vascular arches ; of these, the first, fourth, fifth, and sixth supply the branchiæ, which are filamentous, but not external, like the permanent gills of the lower Amphibia. The second and third pairs, pass as simple channels into the descending aorta, and also give off branches which unite to form a single pulmonary artery, distributed to the largely developed cellulated air-bladder. The single pulmonary vein ends in the sinus of the inferior vena cava.

The preceding descriptions indicate a unity of plan in the circulating organs of the Vertebrate series of animals, as marked as that which may be traced in their skeleton and nervous system—gradual modifications of this plan being manifested in ascending from the lower to the higher animals.

In the *Amphioxus*, the lowest Fish, and therefore the lowest Vertebrate animal, the circulating system retains its Vertebrate type in the arrangement of the principal vessels ; but it presents the singular anomaly of not having a single central heart, but possessing instead, numerous contractile cavities situated in the course of the chief blood-vessels. Beneath the complex branchial chamber, is a contractile vessel, or bulb, performing the office of a ventricle ; from this, as many as fifty pairs of branchial arterial arches arise, at the root of each of which, is a contractile dilatation. These numerous branchial arteries, of which the anterior ones are themselves contractile, end, as usual, in the branchial veins, which are equally numerous, and combine together to form the proper descending aorta, which is placed immediately beneath the chorda dorsalis. The foremost vascular arch, the duct of *Botal*, joins the aorta, without supplying branches to a branchial fringe. The aorta distributes branches to all parts of the body, the veins from which ultimately unite to form two venous trunks, one a portal vein, a part of which is dilated and contractile, and another which represents the vena cava inferior, on which is found a contractile sinus, pulsating rhythmically, and propelling the blood forwards into the rudimentary ventricle already described. The great number and wide distribution of rhythmically contractile

cavities in the circulating system of the *Amphioxus*, suggest a comparison with the multiple hearts, or pulsating chambers, seen in certain Molluscs and Annulose animals. Its blood also contains only colourless corpuscles.

In the Non-vertebrate animals, the blood, and the organs of its circulation, where they exist, are peculiar, and distinguished from the same parts in the Vertebrata. The blood, in the higher forms of these animals, is corpusculated, but its corpuscles are not smooth and coloured with cruorin, like the red corpuscles of the Vertebrata, but, even when the blood itself is tinged, they are usually colourless and granular, like the white blood corpuscles and lymph corpuscles of the Vertebrata. Sometimes, however, they are flattened, discoid, or even angular; and occasionally they have a bluish or greenish tint. In the simplest of these animals, the blood contains only granules.

This common nutritive fluid, or blood, has, indeed, been regarded by some as corresponding rather with the lymph, and the vessels, in which it circulates, as homologous rather with the lymphatic system of the Vertebrata. It is certain that no other vessels corresponding with lymphatics, exist in the Non-vertebrate animals; and no lymphatics have been detected in the *Amphioxus*, which has only colourless corpuscles. The vessels in which it circulates, present this great peculiarity as contrasted with the circulating apparatus of the Vertebrata, that they no longer form a continuous series of well-defined tubes, or true bloodvessels; but, even in the highest forms, and, to a still greater degree, in the lowest forms, the blood passes from such definite vessels into spaces lying, as it were, between the viscera and tissues of the body, furnished doubtless with a lining membrane, but not having otherwise distinct walls or coats. In the higher of these animals, these spaces form spongy recesses, *sinuses*, or *lacunæ*, and in the lower forms, merely *peri-visceral* or *inter-visceral* spaces.

Connected with the true vessels, in many of the higher forms, there are found one or more rhythmically pulsating contractile cavities, which are therefore called hearts; sometimes these are unilocular or ventricular, sometimes bilocular, or auricular and ventricular; sometimes they are multilocular. One of these hearts only can be regarded as homologous with the heart of the Vertebrata, in some of which animals, as in the bat, the eel, torpedo, myxine, and *amphioxus*, for example, portions of the venous system are also pulsatile. Pulsating cavities also exist, as we have seen, in certain Reptiles, Amphibia, and Fishes, in connection with the lymphatic system, viz. the lymphatic hearts.

When the heart in a Non-vertebrate animal is single, it is, as a rule, placed on the dorsal aspect of the body, *i.e.* on the surface opposite to the one upon which the nervous axis is found; it is, moreover, *systemic*, or sends the blood to the various parts of the body, including the liver, and not to the respiratory organs, which only receive the blood as it is returning from the body to the heart. This is the reverse of the arrangement met with in Fishes, in which the heart is *respiratory*. In the Fish, the heart receives and transmits deoxygenated blood, whilst in the Non-vertebrate animal it receives and transmits an oxygenated fluid. When the heart is bilocular, it is constricted externally, and presents a delicate projecting border or valve between the auricle and ventricle. When the

heart is multiple, the supernumerary ones are always simple or respiratory, and are placed upon the veins near the respiratory organs, any modifications of which, as in the Vertebrata, necessitate changes in the arrangements of the vascular system. A portal venous system never exists, the liver being always supplied by the systemic arteries. The vessels are named arteries and veins, according to the direction of the current within them, and not from their structure; for distinct coats, like those of the arteries in the Vertebrata, are not recognisable. Though extremely delicate valves are present in the heart, they are not found so regularly disposed in the veins, as in the Vertebrata. Sometimes, a pericardium exists. True capillaries, provided with distinct walls, and intermediate between the finest arteries and the finest veins, have not been demonstrated, and in most instances are certainly absent; but, the arteries pour out the circulating corpusculated fluid, into lacunæ, or interstices, between the organs or elements of the tissues, from which it is collected into venous sinuses and trunks.

Mollusca.—The most perfect condition of the circulatory system, in the Non-vertebrate animals, is met with in this Sub-kingdom, and in the Class Cephalopods. In the cuttle-fish, for example, there is found a *systemic* ventricular heart, provided with valves at its orifice; it is usually rounded, has strong muscular walls, and even internal columnæ carneæ. Arteries proceed from it to all parts of the body, excepting to the branchiæ or gills, the liver even receiving branches. The blood is returned into a large vein, or venous sinus, which is surrounded by a remarkable cellular organ filled with blood, and from which symmetrical lateral branches, two or four in number, according to the number of the gills, proceed to those organs, each presenting, as it enters the gill, a pulsating dilatation, or so-called branchial heart, which helps to propel the blood through the gills. From the gills, the blood is returned into large venous sinuses, which, being contractile, act as auricles, and thence passes into the ventricular systemic heart already described. In the Pteropods and in the Gasteropods, there is but a single heart, which is always systemic, distributing its contents by one arterial trunk and numerous branches, to the body and liver, from which, having passed through *lacunæ* or spaces, it is again collected by veins, and by them conveyed to the respiratory organs; from these, it is collected by other canals, the branchio-cardiac veins, and is so brought to the heart again. In the terrestrial Pulmogasteropods, as in *Helix*, the venous blood from the body, passes through small vessels on the walls of the pulmonary air sac, and is then collected into a larger vessel, which conveys it to the heart; whilst in the aquatic Branchiogasteropods, as in *Doris*, the blood returning from the body, is carried, by special vessels, into the gills, and is then conveyed, by other vessels, back to the heart. In both kinds of Gasteropods, the heart consists of an auricle and ventricle, between which there is found a distinct but minute valve, which serves accurately to direct the course of the circulating fluid. In the Lamelli-branchiata, the heart, usually single, but sometimes double, in correspondence with the bilateral arrangement of the parts of the body of these animals, and often perforated by the intestine, is placed in a pericardium, situated near the adductor muscle, which closes the shell; when single, it has sometimes one and sometimes two auricles, connected with its simple ventricle; when the heart is double, each has only one auricle.

Molluscoida.—In these animals, the circulatory organs become still more simple, or even disappear. Thus, in the Ascidioida or Tunicata, although the bloodvessels, or blood sinuses, are very complex on the walls of the peculiar respiratory atrium, the heart itself has no valves between its dilated parts or chambers, and the blood is propelled by opposite peristaltic actions, separated by an interval or pause, first in one direction and then in the other; hence the heart is sometimes systemic and sometimes respiratory, and each chamber is sometimes auricular and sometimes ventricular in function. In the compound Ascidioida, it is stated that the vessels of one animal, are connected through the footstalk or common "stolon," with those of the others belonging to the same cluster. In the Brachiopoda, there is still a proper simple heart, sometimes, it is said, two; but the circulating system is considerably reduced in extent; the numerous contractile cavities found in these animals, have not been proved to have any connection with the blood system, but rather to be comparable with the atrium of the Tunicata. Lastly, in the Polyzoa, neither a contractile heart, nor even vessels, have yet been detected; in these soft delicate animals, the nutritive fluids are supposed to permeate the walls of the alimentary canal into the perivisceral spaces, and thence to penetrate every part of the body.

Annulosa.—In the largest animals of this Sub-kingdom, the circulatory apparatus presents the greatest simplification. Thus, amongst the Crustaceans, a single, well developed, muscular, *systemic*, dorsal, heart is found in the lobster; it is placed in the median line, beneath the hinder border of the thoracic part of the shell, and is enclosed in a delicate sac, which, from its resemblance to the pericardium in the Vertebrata, has been so named, but which is, in reality, a venous sinus. From the heart, six systemic arteries are given off to the head, stomach, liver, and caudal extremity; from the lacunæ or spaces between the tissues and organs, the circulating fluid is collected by veins, which end in sinuses placed above the ventral surface; from these, it is conveyed, by distinct vessels, into the gills, there being sometimes contractile dilatations at the base of those organs; having passed through the gills or branchiæ, it is then returned, by the so-called *branchio-cardiac* veins, to the large venous sinus enclosing the contractile heart, into which it enters through valved apertures, and is then propelled into the systemic arteries already described. No cilia ever exist in the interior of any part of the circulating system of the highest or Arthropodous Annulosa. In most other Crustacea, the plan of the circulating apparatus, is the same as in the lobster; but in certain of the lowest forms, the simple heart is replaced by an elongated, and sometimes by a segmented, contractile vessel, or *dorsal vessel*, provided with lateral valved openings, by which the blood enters from an enclosing venous space or sinus. In Insects, the circulatory system presents, as has already been seen in so many instances, modifications adapting it to special forms of the respiratory apparatus. In them, there no longer exist either lungs or gills, but tracheal respiratory tubes ramified through every part of the body. The heart is replaced by a numerously segmented *dorsal vessel*, provided with valves between each segment, contracting rhythmically from behind forwards, and having numerous lateral valved openings, through which the circulating fluid, returned from all parts of the body, enters from

an enclosing so-called pericardial, but really venous, space or sinus. The corpusculated fluid or blood, propelled from the anterior extremity of the dorsal vessel, passes, however, not so much into distinct vessels, as into channels, lacunæ, or spaces, in and between the various organs and tissues of the body, and so comes into relation with the universally diffused tracheal tubes, and then again finds its way back to the pericardial venous sinuses. The chief modification of this system, seen in the Myriapoda and Spiders, consists in the comparative length or shortness, the equal development, and the more or less frequent segmentation of the valved dorsal vessel, in accordance with the consolidation or multiplication of the segments. Thus, in the Geophilida, the number of contractile segments, is upwards of 150; in Iulida, as many as 75; in Scolopendrida, 15 to 21; all are separated by well-formed valves. A small ventral trunk also exists in some Myriapoda. In the Arachnida, the dorsal vessel sometimes consists of only four or five closely packed chambers. These segments, with their interposed valves, are found only in the body of the perfect Insect, and usually number eight or less; in the thorax, the dorsal vessel has no valves, and, in front, it ends in a fine vessel, from which a few branches have been traced. In the microscopic Arachnida, such as the acari, there are no proper vessels, but the nutritive fluid contained in the perivisceral chamber, is moved by means of contractions of the muscles of the intestines and the skin. The scorpion presents the unusual condition of possessing a distinct abdominal vein, proceeding from the tail, and giving branches to the pulmonary sacs.

In the Annelida, the best anatomists agree in doubting the existence of either a contractile chamber or heart, or of a contractile dorsal vessel; the only cavities possessed by them, analogous to the more perfectly developed circulatory apparatus of the Arthropodous Insects, Myriapods, Spiders, and Crustacea, are the perivisceral spaces, lacunæ, and channels, in which a slightly corpusculated fluid has been found. It is in this Class, including the various marine and terrestrial Worms and the Leeches, that those remarkable ramified vessels are met with, extending into every segment and portion of the body, named the *pseudo-hæmal* vessels, which contain, sometimes a colourless, though usually a red coloured fluid, often corpusculated, but the colour of which is not dependent on the corpuscles. These vessels are, at one or many parts, dilated and contractile, and, at certain parts, lined with *cilia*. They always communicate, at some point, by a tubular stem with the exterior; a principal trunk on the dorsal aspect of the body, has been regarded as the representative of the true dorsal vessel of the higher Annulosa; but their homologies are believed to be rather with the so-called *water-vessels* of the still more lowly organised Annuloida, than with the non-ciliated vascular apparatus of the Arthropodous Annulosa.

Annuloida.—In these animals, nothing analogous to a blood system exists, there being neither blood nor true bloodvessels, or lacunar blood spaces. The *water-vessels* of the Rotifera or Wheel-animalcules, of the marine Turbellarian Worms, the Trematode Flukes, the Nematode Threadworms, and the tape-like Tænia and its allies, the Acanthocephali, are ciliated canals, which communicate, at some point, with the exterior, and are, by some, regarded rather as respiratory organs. Neither a heart nor a dorsal vessel has been found in them. The extensive system of

ambulacral and other vessels, possessed by the Echinodermata, also communicates with the exterior, and is, apparently, partly respiratory, and partly locomotive. No heart or bloodvessels have been detected in these animals.

Celenterata.—These are also destitute of blood, cardiac apparatus, and proper circulatory vessels. In the Actinozoa and Hydrozoa, the digestive cavity communicates with the perivisceral or general cavity of the body, from which ramifications, sometimes very fine and numerous, proceed through the disc and other more developed parts. In this way, nutritive fluids get access to all parts of the body, without a circulation of blood.

Protozoa.—The singular, characteristic, slowly pulsating vesicles, which alternately contract and dilate within the soft sarcodous substance of the Infusoria, and Rhizopoda, although they sometimes present radiating ramifications, as in certain Infusoria, are probably respiratory rather than circulatory. In the sarcode of the Sponges, and in the unicellular Gregarinida, there are not even contractile vesicles; and no trace whatever of internal vessels. The circulation of external fluid through the porous substance of a sponge, has, of course, no affinity to a true internal circulation.

NUTRITION.

The general process, by which the microscopic elements of the tissues and organs of the body, are maintained in a healthy condition, and are renovated after disintegration and waste in use, constitutes the function of *Nutrition*.

Nutrition proper, consists in the maintenance of a living part, without any important change of form or size. *Growth* implies a more active nutritive process, resulting in an increase of dimensions. *Development*, besides nutrition and growth, requires evolution, or changes of form. *Reparation* is a nutritive act, which has for its object, the healing of a wound or loss of substance, or the more perfect restoration of an injured or lost part. *Reproduction of a lost part*, is an extreme example of reparation. The act of *secretion* is a nutritive process, in which the products of nutrition are incessantly thrown out from the system. The *reproduction of the individual*, is a special nutritive phenomenon.

In Man and the higher animals, the blood is the common source of the nutrient material for the solid parts of the frame, and, in its rapid circulation through the body, it passes, whilst in the capillaries, within a very minute distance of the ele-

mentary constituents of the various tissues and organs. In yielding this nutrient material, the blood itself is necessarily impoverished, and accordingly is, in its turn, renewed, or nourished, chiefly from the lymph and chyle, both of which are likewise constantly being reformed or renewed. All three fluids, the lymph, the chyle, and the blood, are, however, more or less organised, or at least, the products of organisation. They are, indeed, *fluid tissues*, or *fluid parts* of tissues, being the moveable contents of vessels or tubes formed by the coalescence of hollow elongated nucleated cells. Like the more solid tissues, they are subject to nutritive waste and renovation. In its widest sense, nutrition includes, therefore, the renewal of the lymph and chyle, the renewal of the blood, and the maintenance, or renewal, of the solid tissues and organs of the body.

In each of these processes, there is one common character, viz. that the renewed fluid, or solid, assumes some portion of a nutrient pabulum, different from itself, and converts it into a likeness of itself. Hence the term *assimilation* is employed to indicate the assumption of necessary material into itself, by a fluid or solid tissue. The nutrition of the chyle and blood, or the processes of *chylication* and *sanguification*, are especially included under the term *primary assimilation*, whilst the nutrition of the solid tissues and organs, from the blood, is described as *secondary assimilation*.

Nutrition of the Chyle.

The composition of this fluid, its relations to the food, and the share which the process of absorption has in its formation, have already been described. The nutritive character of that part of the process of chylication, which consists in the absorption of fatty matters, has likewise been indicated. The fatty particles of the chyle within the lacteals, certainly differ from the emulsified fat found on the surface of the intestinal mucous membrane, and the albuminose of the intestinal canal appears as albumen and fibrin in the chyle. Accordingly, these last-named substances, and perhaps also the fat, undergo true assimilative changes, and not a mere absorption, as they enter the chyliciferous vessels. Moreover, the corpuscles which appear, as the fluid advances through the lymphatic plexuses and glands, afford distinct evidence of evolution, organisation, and, therefore, of assimilative power. The

columnar epithelial cells upon the villi, and also the cells of the absorbent vessels and the alveolar spaces of the lymphatic glands, which are themselves developed by the coalescence of hollow nucleated cells, the parietes of which continue to be endowed with special properties of an elective and, therefore, assimilative nature, participate in this process. If, as previously alluded to (p. 180), the process be regarded as *secernent*, the moveable contents of the lacteals, form a secretion, and the entire lymphatic system constitutes a large gland, the secreting tubuli of which begin either amidst the tissues of the body, as lymphatic plexuses, or in the villi of the small intestine, as the commencements of the lacteals; whereas the terminal ducts, of which the chief one is the thoracic duct, open into the great veins at the root of the neck. The vascularity of the septa *within* the lymphatic glands, favours the near proximity of the fresh chyle or lymph, to the capillary bloodvessels; in this way, these fluids may be inspissated by venous absorption, and, moreover, by the action of the arterial blood, the fibrinous matter may acquire the increase which is noticed beyond the lymphatic glands.

Nutrition of the Blood.

The most obvious evidence of organisation in the blood, is the existence of its white and red corpuscles. The very special characters of the latter, which are found only in the blood of the Vertebrata, and which, as we shall see, undergo evolution and decay, afford proof of a further assimilative action, than that which takes place in the formation of the lymph and chyle. The blood, however, owes the maintenance of its extremely composite nature, to other processes than to those of a self-assimilative character: viz. to its losses in the nutrition of the solid tissues of the body, and in the formation of the various secretions; to the changes which it incessantly undergoes, by the entrance into it of new matter, by venous absorption on the one hand, and to the passage from it of effete matter, by excretion on the other; and lastly, to the profound alterations in its character, effected by the action of oxygen in the respiratory process. For these reasons, the subject of the formation of the blood, or Sanguification, will be more conveniently considered hereafter.

Nutrition of the Organs and Tissues.

The nutrition of the various solid parts of the body, *nutrition proper*, or *secondary assimilation*, consists of the following steps or stages.

First, a *nutritive fluid* or *plasma*, exudes from the blood, through the coats of the capillaries, into all the interstices of the tissues. This process may be partly due to porous diffusion, under the influence of the pressure of the blood in the bloodvessels, but partly also to a dialytic movement, regulated by the chemical relations between the liquor sanguinis and the walls of the capillary vessels. As these vessels are everywhere developed in the same manner, from coalesced nucleated cells, the structure, chemical composition, and properties of their walls, are probably the same in every tissue and organ. Hence we may infer that the nature of the exuded fluid plasma, is the same in every part of the body, and, accordingly, that a uniform material derived from the blood, is provided for the nutrition of every part of the system. This nutritive plasma is sometimes supposed to be identical with the liquor sanguinis; but this is doubtful. Fluids effused into various parts of the body, when present in sufficient quantity to be examined, are found to undergo coagulation after they are removed from the influence of the living tissues; they therefore contain a certain quantity of fibrin or fibrinogen, and so far resemble the liquor sanguinis; but they appear generally to possess less albumen and saline matter. Moreover, the liquor sanguinis contains all the ingredients of the blood, whether nutritive or effete, excepting the white and red corpuscles; whilst it is more probable that the exuded plasma, destined for the nutrition of the tissues, consists of a purer nutrient material. Whatever its precise nature, the exuded plasma passes into the finest interstices of the vascular tissues, between the capillary networks, and bathes all the elementary parts of those tissues. Moreover, it penetrates, beyond the vascular parts, all the moist non-vascular tissues, such as the cartilages, the cornea, the capsule and the substance of the crystalline lens, and, likewise, probably even reaches the intervals between the cells of epithelial and epidermoid tissues. The essential difference between a vascular and a non-vascular tissue, consists in the relative distance of their microscopic elements from the nearest capillary vessels, and, therefore, in the space through which the plasma has to pass from those

vessels, before it penetrates the tissue. All the tissues, indeed, whether vascular or non-vascular, whether penetrated by capillaries or not, are, strictly speaking, *extra-vascular*, that is to say, their elementary parts are outside the walls of the corpuscles. The existence of serous or white vessels smaller than, but continuous with, the capillaries, is not generally admitted; but in certain tissues, secondary nutritive channels may exist, as, for example, the lacunæ and canaliculi of bone, and the tubuli of the dentine, by aid of which the nutritive fluid may be still further distributed. The tubular structure of the connective tissue corpuscles and their processes, and the connection of these with the lymphatics, are not admitted.

The *second* stage of the nutritive process, consists in the exercise of a certain selective act, or so-called elective affinity, by the elementary parts of the tissues and organs, by which they assimilate to themselves such portions of the nutritive fluid as are suitable, either without or with further change, to renew, molecule by molecule, their disintegrating substance. The nucleated cells of the epidermis and epithelium, the corpuscles of the grey matter of the brain, the tubular fibres of the white nervous tissues, the complex fibres of the striated muscles, the simple fibrous forms of the contractile fibres or fibre-cells of the organic muscular tissue, and of the fibrous and areolar tissues, and lastly, the consolidated intercellular substance with the remnants of cells imbedded in it, as in cartilage and bone, each derives from the exuded plasma of the blood, and assimilates, its required chemical constituents. The more rapid the waste, the more active is the renovation, both processes being most marked in the muscular and nervous tissues, which produce and regulate all animal movement. This assimilative power of the tissue elements, is the persistent, primitive, nutritive force, inherited from the germ-cell. It is probably alike possessed by every cell, however remote in its descent from the parent cell, and however modified, so as to form parts of a composite animal or tissue, just as it undoubtedly is when a single cell constitutes the entire animal. This germ force, or germinal force, is the essential cause of all nutritive phenomena, as it is of all organisation, whether animal or vegetable. By it, the cellular yeast plant grows and maintains itself in fermenting saccharine solutions, the larger fungi feed themselves upon juices derived from decaying organic matter in the soil, the various tissues of the more complex flowering plants are formed and supported out

of a common pabulum, the sap; and, in the Animal Kingdom, the unicellular Gregarina, the sarcodous Rhizopod, the proteiform Amœba, the soft-bodied Cœlenterata, with their ectoderm, endoderm, and intermediate tissue, and, lastly, all the complex tissues and various organs of animals higher in the scale, and of Man, are duly nourished. By this, the nerve tissue attracts from the plasma outside the capillaries, its essential fatty and other constituents, the muscular fibre assumes the materials for fresh syntonin, the cartilage those for its chondrin, the bones, their peculiar animal and earthy materials, and so on, of every other tissue of the body. The act of nutritive assimilation, is said to imply a *metabolic* effort, operating in regard to the substance of the tissues, whilst in development, or evolution, this is associated with a *metamorphic* effort, which determines their form. Both kinds of nutritive phenomena are manifest chiefly, probably exclusively, in certain *areas* around the nuclei, or corpuscles, of the cells, the so-called *germinal centres*, which are therefore known as areas and centres of nutrition. The few cases in which, as in elastic ligaments, the nuclei or corpuscles are said to be absorbed, may only be apparent exceptions to the rule. Certain conditions of the blood, and of the temperature of the body, are essential to the occurrence of nutritive actions. They are most active at the commencement of the life of any animal, and gradually decline as that advances, until the power to maintain the body, is overcome by the forces which lead to its degeneration and decay.

In reference to the act of assimilation, and, indeed, of original organisation, it is remarked by Graham, that colloidal substances may not only be regarded as forming the essential plastic elements of the body, capable like all colloids, of existing both in the liquid and in the pectous condition; but that, in the organising and assimilating process, these colloidal bodies do pass from the liquid into the pectous state, as they assume the form and characters of tissues and organs. The slow rate of these colloidal changes, harmonises with the gradual and periodic nature of the processes of growth and disintegration, with which all vital phenomena, whether of vegetative or animal life, are connected. The *ENERGIA*, or force, peculiar to colloids, may be, indeed, the primary source of the physical force appearing in the phenomena of vitality (Graham).

Thirdly, the result of the act of assimilation by the various tissues, is to leave a residual fluid in the interspaces of the tissue-elements, outside the capillary vessels. The nature of this interstitial fluid, unlike the common plasma of which it is a residue, must differ in the different tissues, as, for

example, in muscle, brain, liver, and connective tissue. This residual portion of the nutritive plasma not being effete, but merely defective in composition, is supposed to enter the commencing lymphatics, and thus to be returned to the blood through the absorbent system. Probably, as already indicated, this is accomplished by true assimilative acts, on the part of the lymphatic vessels and glands, owing to which, certain appropriate constituents only of the residual portion of the plasma, enter the commencing lymphatics. It is remarkable that these vessels are most abundant in the connective tissue, in which the residual part of the plasma is least altered, and few or absent in muscle and brain, where the greatest modifications are effected in it, and where, accordingly, it is less fitted to form fresh lymph. It might be conceived, without adopting Virchow's and Recklinghauser's views as to the origin of the lymphatics in the connective tissue corpuscles, that the areolar tissue in, and between, all the organs of the body, acts as a sort of spongy bed or matrix, into which the residual part of the nutritive plasma escapes, and so may be more easily taken up by the lymphatics which abound in it.

Fourthly, the final residue of the exuded plasma, which is neither used by the tissues of the body, nor absorbed by the intruded lymphatic vessels, remains to be accounted for. This must be conveyed, probably, by simple and unavoidable dialysis, without power of selection or rejection, into the venous half of the capillary network, and the minute venules immediately adjoining. No other destination can be assigned to it, and unless it were carried off, dropsical accumulations, or effusions, would take place in the tissues. From this, it would appear, that whilst the still serviceable parts of the residual plasma, left after the nutrition of the other tissues, are restored indirectly to the blood, by lymphatic absorption and assimilation, the unserviceable, or final, and no longer nutritious, residuum, passes into the circulation directly, by means of venous absorption.

Lastly, with this final residuum of the nutritive plasma, there are necessarily mingled the products of the disintegration of the tissues, which always accompanies their action. Without waste there is no use, and without use there is no life. It is the loss which living and acting tissues undergo, which necessitates their nutrition; and whilst new pabulum is brought by the arterial blood, which yields a nutritive plasma through the walls of the arterial half of the capillary network,

from which plasma all the tissues receive respectively their requisite materials, the products of their waste would seem first to become dissolved in the ultimate residuum of the plasma, and with it, to enter the venous blood, through the walls of the venous half of the capillaries and of the minute veins. These products of waste are really effete, and no longer fit for the purposes of nutrition; physiologically, they are the result of a process of *de-nutrition*, and, chemically considered, of a process of *oxidation*, of the tissue substance. It is these which impart to the blood, its *positive* venous characters. Thus, venous blood is more watery; it contains less nutritive matter; it is also rendered impure by containing the waste products of the tissues, the chief of which are carbonic acid, lactic acid, and urea. The former of these, as we shall hereafter see, is replaced by oxygen in the lungs, and so a negative defect in venous blood, the want of that stimulating agent, is supplied. Here, also, the carbonic acid is given off; whilst the lactic acid, phosphates, and urea, are eliminated, or cast out of the blood, by the excretory glands, especially by the skin and kidneys.

The five stages of the nutritive process, though here separately described, viz. the exudation of the nutritive plasma from the blood, the assimilation of parts of this by the tissues under repair, the absorption and assimilation of other portions by the lymphatics, and lastly, the reabsorption of the final residue, together with that of the waste products of the tissues, by the venous capillaries and veins, are, of course, in the living body, simultaneously and continuously performed, and in the healthy condition, with a perfect balance of action. Especially must the removal of the waste products, be incessant, or they would taint the nutritive plasma, and cause inflammation, as in reality occurs in rheumatism and gout.

In the embryo, and in the growing animal, nutrition not only repairs the constant waste of the tissues, but, as already stated, contributes to the formation of new morphological elements, in the processes of development and growth. But, after the body has attained its maturity, growth ceases in most, though not in all, of the tissues. Hence *two* kinds of nutritive processes are noticeable in the adult.

In *one*, not only are the already existing cell-elements, and their secondary intra- or intercellular products, supplied with materials for their special nutrition, until they have passed through all the metamorphoses peculiar to them; but new cell-

elements, or germinal centres, are constantly being reproduced and developed, for the purpose of supplying the place of those which are cast off; these new cells are, in turn, succeeded by others. This process, named *continuous growth*, occurs in the epidermis, nails, and hair, in the epithelial tissues of the mucous membranes and secreting glands, and probably also in the grey nervous substance. Moreover, from the active internal changes of absorption and deposition constantly going on in bone, as indicated by observations on the bones of animals fed with madder, it would seem that new cells are continually being formed in that tissue, and, if so, perhaps in cartilage also. In the nutrition of the blood, there occurs not merely a continued renovation of pre-existing red corpuscles, but also the death and disappearance of a certain proportion of these, together with the reproduction of new ones. In the *other* mode of nutrition, when once a tissue has attained maturity, no new morphological elements are added to it; such is supposed to be the case, with the areolar and fibrous tissues, and with the muscular and nervous fibres. In these tissues, the nutritive process consists merely in interstitial disintegration and deposition, affecting the elements of the perfectly formed tissue, molecule by molecule, so as effectually to preserve the shape and size of a part or organ, as long as the normal or healthy standard of nutrition is maintained. According to this view, even the enlargement of a muscle from exercise, is owing to an increase in the size of the fibrillæ in each fibre, and not to the formation of new fibres, or even of new fibrillæ; whilst muscular emaciation is due merely to a diminution in the size of those elements. It is, however, supposed by some, that, as in bone, so in muscle, new centres of growth, or nuclei, are developed from time to time, and give rise to new fibres, amongst the pre-existing ones, some of which are, on the other hand, constantly undergoing retrograde changes, and disappearing.

In the mode of nutrition by the continuous growth of new cells on the surface, the old elements are cast off directly at the surface of the body, or of some one of its internal membranes; parts of them, however, are sometimes reabsorbed as secretions. In the interstitial mode of nutrition, the products of disintegration, arising from nutritive changes in the substance of the tissue, are taken up, if not by the absorbents, at all events by the bloodvessels, and so enter the blood.

The phenomena of nutrition are necessarily affected,

through the blood, by the quantity and quality of the food, by all the changes which occur in the blood itself, by what is called the general condition of the health, by exercise or the reverse, and by external conditions, such as temperature, mechanical causes, pressure or violence, or chemical agents.

Nutrition is also affected, and modified, by the state of the nervous system, as exemplified by the effect of emotions and other causes, probably in the main, through the action of the vasi-motor nerves regulating the diameter of the small arteries of a part. Perversions of the condition of the nerves or nervous centres, may induce a perverted state of the nutritive processes, both general and local. The formative and nutritive energy is, however, not derived from the nervous system; for it is manifested not only in animals destitute, so far as is known, of any nervous system, but even in plants. Moreover, it begins to act in the ovum, previous to the existence of a nervous system, which system, indeed, is developed by its agency. Of the numerous instances usually adduced, to prove that the nervous system may directly guide, or modify, the nutritive changes in the tissues, independently of its action on the bloodvessels, none are satisfactory, if adduced in the case of animals possessing bloodvessels; for it is impossible, in such cases, to exclude the action of the nerves upon these vessels. But there are animals, low in the scale, such as the Beroë and other Cœlenterata, in which a nervous system exists, without bloodvessels; and, in these cases, any action of the former, upon the nutritive processes, must be direct, and not through the agency of vessels. The increased nutrition or secretion from a part in such an animal, due to a stimulus acting on its nerves, furnishes, unless this is influenced by the contraction of the tissues themselves, the requisite example of such direct action. If so, by analogy, it might also occur in the vascular animals, and in Man.

Certain muscular organs, stimulated through the nerves, such as the gravid uterus of the Mammalia, and the muscles of the frog after the season of hybernation, undergo normal periodic enlargements. In this form of over-nutrition, both the processes first mentioned, usually occur, viz. an increase in the size of the pre-existing elements, or *hypertrophy*, and also an increase in their number, or *hyperplasia*. Budge has actually observed this latter mode of increase, in the muscles of the frog, new fibres being developed from nuclei arising from the old ones within the sarcolemma of the pre-existing

fibres. In such cases, a corresponding increase takes place in the nerves, and new nerve fibres also appear to be developed by aid of the nuclei of the old ones (Kühne). The blood-vessels of such parts must also enlarge—a change not due to simple dilatation, but to a coincident interstitial hypertrophy of the tissue elements of their walls.

Various deviations from the normal standard of nutrition, are met with in the body; they are fertile sources of organic disease, giving rise to the morbid conditions known as *hypertrophy* and *hyperplasia*, *neoplasia*, *atrophy*, *softening*, *induration*, *degeneration*, and *inflammation*, with its consequences.

Hypertrophy and *hyperplasia*, already defined, are usually attributed, either to an over-abundance of certain materials in the blood, suitable to the development of some particular tissue, or to excessive supply of blood, to over-exercise of a part, or to some not understood tendency to an increase of size or growth, by excessive enlargement or multiplication of the tissue-elements. Muscular hypertrophy and hyperplasia, are more common in the involuntary than in the voluntary muscles.

Neoplasia, or the formation of new growths, is referred to a perverted nutrition. Its cause is unknown; though it is attributed, with some probability, to the accumulation in the blood of some similar nutritive material or pabulum, fitted to stimulate their formation, and support their growth and nutrition. The resulting *tumours* are sometimes *homoplastic* or *homologous*, that is, they exhibit a structure similar to that of some normal tissue; or they are *heterologous* or *heteroplastic*, their structure being entirely unlike any healthy texture. Fatty, fibrous, cartilaginous, and bony tumours belong to the former, and tubercle, fibroplastic sarcomas, and cancers, to the latter variety of new formations. These, when once formed, are the seat of continued nutritive changes, more or less perfect and proper to themselves, and maintaining, in the midst of interstitial changes, the character of the abnormal tissue-elements of each growth.

Atrophy, or the gradual or rapid wasting of a part or tissue, depends on general defective nutritive activity, an unhealthy condition or deficient supply of blood, want of exercise in a part, or loss of intrinsic nutritive power. Atrophy may be general, as that which follows deficiency of food or actual starvation, or partial and local, as that which occurs in the fatty tissue, when no fatty, amylaceous, or saccharine food is eaten, and the blood is destitute of fatty matter.

Softening, *induration*, and *degeneration*, imply not only defective, but more or less altered, nutrition. The first consists in a liquefaction of the tissue-elements; the second and third, in depositions, in or about them, of albuminoid or amyloid substance, or in an actual conversion of the proper albuminoid or gelatin-forming material of the tissue, into fatty matter—a change not unfrequently seen in muscular tissues, especially in those who indulge in alcoholic beverages. In certain cases, fatty degeneration prepares a tissue, or some morbid deposit, the result of inflammatory or perverted hypertrophic or hyperplastic action, for more easy absorption and removal from the body; sometimes this and other changes destroy tumours, and so lead to exhaustion and death.

Inflammation is essentially an abnormal or altered nutritive process.

It commences in some altered relation between the nutritive qualities and reactions of a tissue, and of the blood, or its exuded plasma; the normal nutritive changes are arrested; the unused plasma soon becomes excessive in quantity; new products are stimulated into growth, including, essentially, cells formed by multiplication of the pre-existing connective tissue corpuscles. Moreover, the condition of the blood, and of the capillaries, very soon becomes changed; the blood becomes less fluid, and the vessels distended and enlarged, causing a state of congestion; the red corpuscles of the blood in the part, cohere, and at last become motionless or stagnate, *stasis* being produced; the white corpuscles increase in number in the blood generally, owing it is supposed, to over-activity of the commencing lymphatics of the inflamed part. Lastly, the nerves of the part are excited by these changes, and by the disturbance in their own nutrition. The chief obvious results and evidences of inflammation, are swelling, redness, heat, and pain; but these are effects, and not even essential characters, for one or more of them may be, under certain circumstances, absent.

Inflammation may end favourably in *resolution*, which consists in the absorption of the exuded material, and of the new products stimulated to growth by it. These may, however, undergo rapid increase, and form solid and morbid *plastic deposits*, or fluid *pus*, abounding in corpuscles like the white blood corpuscles, and so give rise to induration, inflammatory thickening, or *suppuration*. Collections of pus, surrounded by plastic deposit, constitute *abscesses*; these, by progressive absorption of their coverings, may reach the surface, and burst. A further result of inflammation, is *ulceration*, which consists in the *molecular* death, and gradual softening and falling away, of a highly inflamed part of the surface of a tissue or organ, causing a loss of substance, or sore known as an *ulcer*. *Gangrene*, or *mortification*, is the complete *molar* death of a part, dependent, sometimes, on excessive inflammation, causing obstruction or occlusion of the larger or smaller bloodvessels, or an actual destruction by violence, heat, cold, or chemical agents. The body may also be wounded, or parts even completely detached from it.

As inflammation and its consequences, are essentially derangements of the nutritive process, so, on the other hand, all the *reparative* phenomena seen in the living animal body, which tend to preserve life, consist in most remarkable and energetic manifestations of modified development, growth, and nutrition. Thus, the cavity of an abscess, is chiefly closed by the collapse of its sides; but, also, by a new and very vascular, soft, red formation, in its interior, known as *granulations*, which are developed from new cell-elements, partly metamorphosed into connective tissue, and partly into bloodvessels, whilst certain of the cells escape as pus; ultimately, these granulations cohere, and the orifice being closed up, is covered by new epidermis, or by *cicatrization*. An ulcer, or a wound is filled up, and healed, in a similar manner, by granulation, suppuration, and cicatrization, the resulting mark being named a scar, or cicatrix. The temporary covering, or natural dressing of an ulcer, known as a scab, consists of dried exuded materials and pus. Gangrenous parts are detached, separated, and thrown off, by a remarkable ulcerative process, or molecular decay, occurring, not in the dead parts, but in the living parts in immediate proximity to them; when these are detached, the raw surface is healed by granulation, suppuration, and cicatrization.

The *healing* of actual *wounds*, differs according to the extent, depth, and relative proximity of the surfaces, and the degree of their exposure to the air. It may sometimes occur by *immediate* or *direct union*, as in the healing of subcutaneous wounds, without any manifest inflammation, and, it is said, even without any observable exudation of intermediate or uniting plastic matter. Sometimes this may also occur in the healing of external cut surfaces, which have quite ceased to bleed, and can be maintained in accurate and immoveable apposition, and from between which air can be totally excluded. Most frequently, however, healing is accompanied by more or less inflammatory action, and the formation of a new uniting substance; this constitutes union by *adhesive inflammation*, or by the *first intention*. In this mode of union, plastic matter is exuded, new cells are formed and converted into connective and capillary tissue, and so the divided, but apposed surfaces, are joined. When the wound is deep, or the loss of substance is great, or the apposition of the surfaces impossible, or when, from any other cause, the adhesive inflammation does not happen, then the surfaces granulate and suppurate, like those of an ulcer or abscess, and when these have closed up the cavity, cicatrisation ensues. The extent and mode of reparation in each tissue, and in various animals, will be explained in the Section on Development. In all cicatrices, or other repaired parts, nutritive changes afterwards go on, resulting, as in the healthy tissues, in the maintenance of the form and characters of the newly developed tissue or scar.

Offices of the Blood and of its several Constituents in Nutrition.

The general fact, already indicated, that the blood is the source of all the nutrient material for the solid tissues of the body, is illustrated in many ways. Thus, the activity of the nutritive process, is coincident with the quantity and quality of the blood supplied to a particular part or organ. Unless it be constantly supplied, through the absorbent system, with fresh nutriment from food, it becomes itself impoverished, showing the demand made upon it, by the nutritive wants of the solid tissues. Ligature of the arteries of a part, is followed by a diminution in its size, owing to defective nutrition; and not only does complete closure of the arteries accomplish this, but even their compression. There are instances in which an increased supply of blood, through enlargement of the arteries, occurs as a natural phenomenon in the living body, and, in such cases, this *determination of blood*, as it is called, is accompanied by an increased growth in the part or organ supplied, as exemplified in the annual development of the antlers of the stag, and in the periodic enlargement of the mammary glands in the Mammalia, for the supply of their young with

milk. Again, the falling of the antlers, and the disappearance of portions of healthy bone, in the ordinary nutrition of that texture, are always preceded, or accompanied, by a gradual shrinking and final closure of the vessels which nourish them, by the filling up of the Haversian canals of the bony tissue; thus, nutrition is arrested, as the supply of blood is cut off. Lastly, hæmorrhages, or bleedings, are followed eventually, by diminished nutrition of the body. But the immediate effects of severe hæmorrhage, are most remarkable. The functional activity of the muscular and nervous systems, the exercise of which also demands rapid nutritive changes, is either enfeebled, suspended, or lost. Every sensation, perception, emotion, or volition, and every movement, is accompanied by disintegration of nervous or muscular tissue, or of both; these tissues are maintained in a fit state for action, by a due supply of oxygenated blood and nutritive plasma, and the several changes which occur in them and in the blood, are retrogressive chemical decompositions, accomplished through the agency of the oxygen conveyed in the latter. Accordingly, a loss of blood from hæmorrhage, a diminution of that fluid from pressure on the vessels, or an arrest of the circulation from ligature, or other causes, is followed by a diminution, suspension, or annihilation of the functions of a muscle or nervous centre. Similar results ensue from serious alterations in the quality of the blood, as when the proportion of oxygen in it, is deficient, or when carbonic acid is in excess, as is seen in the immediate loss of consciousness and muscular power, which follows the arrest of the decarbonising and oxygenating processes of respiration. The nutrition of the body generally, also becomes defective, from a continually diminished supply of pure air, owing to the blood not being then duly oxygenated and purified. Finally, the influence of the blood, in stimulating and nourishing the tissues, is directly proved by the remarkable resuscitating effects of injecting that fluid into the veins of persons or animals, previously deprived of blood by accidental or intentional hæmorrhage, the powers of the whole system which have previously been suspended, being, in this way, almost instantaneously restored.

The nutritive, stimulating, and resuscitating powers of the blood, depend on the chemical constitution of the liquor sanguinis, and on the number, composition, and properties of the corpuscles which it contains; and the special offices of the different parts of this fluid, for the processes of nutrition, may

be referred both to its morphological and chemical constituents, which have already been described (Vol. I. pp. 62, 90).

The white corpuscles appear to serve, at all periods after birth, for the renovation of the red or coloured ones. They are very abundant in sickly and ill-fed persons; also in anæmia, in inflammations, and in certain diseases of the spleen, probably because they do not then undergo the usual change into red corpuscles, and so relatively accumulate in number.

The *red corpuscles*, by virtue, as it would seem, of the colouring matter, or *cruorin*, are the great carriers into the system of oxygen, which displaces carbonic acid from the blood during respiration, as will be explained in the section on that subject. The substance usually known as hæmatin, is a product of the decomposition of cruorin, by the action of acids or caustic alkalies. The hæmatin of Lecanu is a highly coloured albuminoid substance, containing iron; its chemical relations with the myochrome of muscles, the pigment of the choroid and iris, of the hairs and skin, in both the dark and fair races of mankind, and also with the colouring matters of the bile, the urine, and the supra-renal bodies, may indicate some nutritive relations between it and them; it may perhaps be formed in the spleen, or in the lungs, and may be dissolved, in minute quantity, in the nutritive plasma, and so find its way chiefly to the muscles and hairs, in the colouring matter of both of which, iron is also found. The red corpuscles also probably furnish, by their solution, continuous supplies of albuminoid matter to the liquor sanguinis, the globulin of the corpuscles having a close resemblance to albumen and syntonin. The fact, however, that the red corpuscles contain most of the potash, whilst the liquor sanguinis contains most of the soda, of the blood, may indicate that the muscular tissue which also abounds in potash, may receive special nourishment from these; and, as they also contain a phosphorised fatty matter, they may have special nutritive relations, direct or indirect, with the nervous substance. The quantity of the red corpuscles in the blood, is certainly greatest in healthy and vigorous persons. These corpuscles are also most abundant in the hot-blooded Birds, not quite so numerous in the Mammalia, the temperature of which is not so high, and much fewer in the cold-blooded Reptiles, Amphibia, and Fishes. Their proportion in the blood, is in direct relation, not only with the temperature of the body, but also with the general activity and energy of the muscular and nervous apparatus. From this

cause, the ratio of the general solids to the water of the blood, shows similar proportions in the different Vertebrate Classes.

The special nutritive office of the liquor sanguinis, must be explained by its composite chemical constitution. Its peculiar physical character of smooth viscosity, due to the albumen, and particularly, it is said, to the fluid fibrin which it contains, is highly favourable to the easy passage of the blood along minute channels like the capillaries, without its exuding too freely through their walls, and perhaps also to the uniform suspension of the red particles in it. A tendency to exude in undue quantity through the coats of the vessels, is probably favoured by a diminution in the amount of fibrin, as well as by like changes in the proportions of the albumen and the salts.

The uses of the particular chemical constituents of the blood, as a whole, require further consideration. The *albuminoid* principles of the blood, its most abundant constituents, include the globulin of the red corpuscles, the albumen of the white corpuscles, and that held in solution in the liquor sanguinis; this latter is said to be chiefly derived from, or prepared by, the blood corpuscles, the globulin of which is believed to escape into the liquor sanguinis, either through their thin envelopes, or after their solution. These albuminoid substances are of the highest nutritive value; for they, or their derivatives, are found, in larger or smaller quantity, in all the tissues and organs of the body, both in the microscopic cell elements and the intercellular substance, appearing as albumen or syntonin in the nervous tissues, as syntonin in the muscles, much changed, as a gelatin-, or chondrin-, yielding substance in the fibrous and areolar tissues, bone, and cartilage, and as elastin in the yellow ligaments and other elastic tissues. Gelatin is not found in the blood itself; but when digested, it is converted into a gelatin-peptone, and so becomes absorbed as we have seen, but in what state, is not yet known; nor is its destination in the nutritive processes of the body certain. Either it may serve for the direct nutrition of the gelatin-yielding tissues; or, and this is very probable, it may, by itself undergoing oxidation, conserve other more important tissues, and, at the same time, maintain the temperature of the body. Its efficacy as administered in jellies, beef-tea, and broth, in cases of sickness, especially indicates its importance as an article of diet. Furthermore, the albuminoid substances such as salivin, pepsin, pancreatin and casein, found in many most important secretions, must be derived from the albumen

of the blood. The quantity of these formed in the day, is considerable, but those contained in the digestive fluids, are quickly absorbed into the blood again. Though so highly nutritive, and absolutely essential to the economy, albumen, considered as an organisable substance, has no metamorphic power; though it affords a fit material for metamorphic action.

The *fibrin* of the blood, was formerly supposed to be specially intended for the nutrition of the muscles, their albuminoid constituent, syntonin, being considered to be identical with the fibrin of the blood. It is now believed that the fibrin is not so essential for nutritive purposes as the albumen, and the small proportionate quantity in the blood, as compared with other albuminoid bodies, viz. about 1 to 90, is in accordance with this idea. Fibrin is more highly oxidated, or contains more oxygen, than albumen; hence it may be a degraded form or condition of albumen, exhibiting a retrogressive change into some still lower compounds. As already mentioned, it may assist in maintaining some essential physical characters of the blood; and, lastly, it plays a highly important part, in causing the coagulation of this fluid. To this change in the blood, the character and causes of which will be hereafter discussed, the first closure of the orifices of bleeding arteries and veins is often due, and further hæmorrhage is thus arrested. Moreover, in most acts, especially in the union of divided parts, and in the healing of sores, the fibrin contained in the exuded plasma, coagulates, forming the first bond of union, and a matrix in which nuclei or nucleated cells are developed; further reparative changes then ensue, according to the tissue which is the seat of reparation. But the coagulation of exuded fibrin in the living animal economy, though often beneficial, sometimes induces injurious consequences to the system, as, for example, in adhesive inflammation of the peritonæum, by which the intestines and other organs become adherent, or constricted by bands of newly-formed tissue, which interfere with, or altogether hinder, their proper movements and actions, in similar adhesions between the lungs and the side of the chest, between the heart and the pericardium, and also, and still more strikingly, in the attachment of the iris to the capsule of the lens, or other parts within the eyeball, even causing blindness by the complete closure of the pupil. Not only fibrinous exudations from the vessels, but even extravasated blood itself, may coagulate within the tissues; by some,

it is maintained that it may itself become the seat of subsequent organisation.

The *fatty matter* of the blood, which is of various kinds, is highly nutritive, scarcely any tissue being altogether destitute of fat in larger or smaller quantity. Phosphorised fats especially abound in the nervous substance, and exist in the red corpuscles of the blood. Fat is always present in newly-forming tissues and newly-forming cells, the nuclei of which often contain fatty particles surrounded by an albuminous deposit. Fatty matter is found, too, not only in the fluid parts of the blood, but also in the organised morphological elements, the blood corpuscles, especially in the red ones. It was observed by Ascherson, that when oleaginous substances are agitated with albuminous solutions, the fatty matter breaks up into minute particles, surrounded by a film of albumen; and he believed that some such physical combination of oleaginous and albuminous matter, might explain the formation of the lowest morphological elements, such as granules, and even of certain nuclei, though not the origin and growth of cells themselves. Without adopting this view, it may be admitted that fatty matter is essential to all nuclear and cell growth, and to every process of tissue formation, even to the assimilation of albuminous matter; for fat globules are always present in the ovum or germ-cell of every animal. Fat is necessary to the formation of certain secretions, as of the bile, milk, and sebaceous matters of the skin. The bile contains a very large quantity of fatty acids. It is possible that fat itself may be derived from other constituents, as from albuminoid, amyloid, or saccharine matter. The great value of oleoids, especially of such as are easily digested, absorbed, and assimilated, is exemplified in the beneficial action of cod-liver oil in tuberculous diseases. Besides its use as a nutritive substance, the fat of the blood is probably also constantly subject to oxidation, for the production of animal energy and heat. But there are other substances in the blood, which are probably even more easily oxidated than its fats.

Arterial blood does not contain any *amyloid* substance; but traces of *sugar* are present in it. This is formed in the liver, but also, it would seem, in the muscles, and probably in other parts; it is also taken up from the food. Nevertheless, the quantity present is small; it is, perhaps, less concerned in nutrition than in the production of heat and motion by its rapid oxidation. It may, however, take part in the formation

of milk. The inosite, lactic acid, creatin, and creatinin, and other extractives, are probably not so much directly nutritive, as stimulating, or excretive; they all represent stages of chemical retrogression, from less to more oxidised compounds, and may, by their further oxidation, assist in the evolution of heat. As completely effete and non-nutritious, or even poisonous, must be classed, the urea, detectable, in minute traces in the blood, as well as the ammonia which escapes from it when it is drawn, and the uric acid, all of which are excretory substances.

The *salts* of the blood are said to prevent its decomposition, and also to regulate its chemical characters and its specific gravity or density, so as to adapt it to the healthy condition of the liquor sanguinis and blood corpuscles floating in it. It is well known that certain salts are preservative, and, likewise, that if the blood corpuscles be suspended in a fluid of too low a specific gravity, they immediately become distended, a process of endosmosis going on into them; whereas, if the fluid be of too high a specific gravity, they shrink by exosmosis. But neither of these supposed uses, explains the great variety of the saline constituents of the blood; for one saline substance alone, say common salt, would have sufficed for both these purposes. Several uses are probably served by this variety. Thus, some salts, perhaps, are necessary for the maintenance of the properties of blood; others are destined for the nutrition of certain tissues, or the formation of certain secretions; whilst others again appear to be the result of the disintegrating and oxidating processes going on in the tissues and organs of the body, during the exercise of their respective functions.

Thus, *common salt*, or *chloride of sodium*, appears to be present in the blood of all animals, and in every tissue. Its great importance is evidenced by the tenacity with which it is held in the bodies of animals, and accumulates in their blood and tissues, even when, as in the case of the herbivorous species, the food which they consume, contains comparatively minute traces of it. The strong necessity and appetite for salt, felt by the herbivorous Mammalia, is shown by their licking lumps of that substance, or boiled bones, scattered about their pastures; and also by the periodical migrations of herds of cattle to the salt districts in South America—facts which indicate that salt is indispensable for the healthy condition of the blood, and of the tissues which are nourished from it. It would seem, indeed, that chloride of sodium is associated with every important act of

tissue formation and change. Of the secretions, all exhibit minute traces of salt; but the gastric juice, in particular, contains an acid—the hydrochloric—derivable only from the salt of the blood; for the quantity of chloride of potassium, as compared with the chloride of sodium, in the blood, is so small, that it may be inferred that the latter is the source of this acid of the gastric juice. The large quantity of soda present in the bile, in combination with its fatty acids, is probably also derived from the common salt in the blood; the separation of the chlorine from this, for the formation of the hydrochloric acid of the gastric juice, may be accompanied by the transference of the sodium, in the shape of soda, to the hepatic cells, for combination with the biliary acids. Again, the lime salts in the blood, chiefly the phosphate of lime with carbonate, held in solution in lactic and carbonic acids, are highly important nutritive substances, being found in all growing tissues; as is well known, they are especially deposited, as a consolidating material essential to the formation of the skeleton, and of the dentine and enamel of the teeth. Of these tissues, although the enamel undergoes no nutritive change after it has been formed, and the dentine very little, the bones are constantly exhibiting very active metamorphoses. Carbonate of lime, phosphate of magnesia, and silicates and fluorides, are usually associated with the phosphate of lime.

But there are other salts, such as the *phosphates* and *sulphates*, both of potash and soda, which, probably, are derived from the oxidation of the phosphorus and sulphur contained in the phosphorised fatty matters found in the red corpuscles, and especially in the nervous tissues, and in the sulphuretted albuminoid substances existing in muscle and brain. The phosphorus and sulphur in these compounds, are either directly oxidised, and combined with soda or potash, or else they pass first into intermediate substances, such as the highly sulphuretted substance, the taurin of the bile. If carbonates of soda or potash exist in the blood, they also are probably not nutrient, but represent the results of chemical retrogressive metamorphoses in the blood and tissues. Moreover, the phosphate of soda, which has an alkaline reaction, and any carbonate of soda which may be present in the blood, serve very important and special uses in that fluid, helping to dissolve the albumen, to favour the chemical oxidation of many substances in the blood, the absorption of gases, and the passage of the nutrient plasma through the walls of the capillaries.

The salts of potash are, it would seem, absolutely necessary to the nutritive changes which occur in muscular tissue. The importance of potash especially, in preserving the healthy condition of the blood, perhaps by determining or aiding the chemical actions necessary for that end, is illustrated in the beneficial effects of fresh vegetables and fruits, as articles of food. They especially abound in neutral or acid salts of potash; and a diet from which they are absent, if long used, induces that condition of the blood, which causes scurvy or *scorbutus*. The employment of neutral salts of potash, aids, at least, in the cure of this disease; but it is more effectually remedied by the use of lime juice, potatoes, or fresh vegetables themselves. Hence, perhaps, a vegetable diet operates on the blood and tissues, in some other mode than by the potash in which it abounds.

Of the *gases* contained in the blood, the nitrogen is probably indifferent, and without special office, its relative proportion constantly varying, both in arterial and venous blood. On the other hand, the *oxygen* must be regarded as an agent of the highest importance. It purifies the blood, and, dissolved in, or combined with, the cruorin of the red corpuscles, is by them carried through the system, and operates on all the tissues. Its action is not so much to contribute to the formation of tissue, by being combined with, or *fixed* in, the tissues in the act of morphosis, as to stimulate the tissue elements, especially those of the nervous and muscular tissues, to their proper functions, causing chemical changes or oxidations of their substance, or of the blood passing through them, essential to their action, and more or less destructive of their substance. So essential is oxygen for this purpose, that the deprivation of it, for but a few minutes, is fatal to the life of these two tissues. As to the *carbonic acid* gas of the blood, not only is it neither nutrient nor stimulant, but it is the chief ultimate product of the oxidation of the tissues, being probably derived, however, from the oxidation of intermediate compounds, into which the materials of the used-up blood and tissues break down. It is the ultimate effete form in which most of the decomposed carbonaceous substances are eliminated from the body. It is an impurity in the blood, which requires to be incessantly expelled from it, and, indeed, is so displaced by the aid of the oxygen in respiration. Under its influence, the scarlet colour and the other properties of arterial blood, are changed, and the blood becomes dark and venous. It is so detrimental to the life of both the nervous and muscular tissues, that, in cases of

asphyxia, in which it ceases to be eliminated by the lungs, death seems rather to take place from the poisonous nature of the accumulated carbonic acid, than from the mere absence of the nutritive, or stimulating and vivifying, oxygen.

The nutritive properties of the blood, *differ* according to many circumstances, being influenced by the character of that fluid, the age, sex, temperament, habits as to exercise and occupation, the constitutional state, and the nature of the food. Thus arterial blood is more nutritive and stimulating than venous blood, which will not long support life, especially that of the nervo-muscular apparatus. Arterial blood not only contains more oxygen, and less carbonic acid; but its liquor sanguinis is richer in fibrin, and its corpuscles contain more cruorin and saline substances, and much less fat—their total solid matter being less than that of the corpuscles in venous blood. The fluid part of arterial blood, also contains less fat, but more saccharine and extractive matters. Again, the blood is less rich in childhood than before birth; its corpuscles increase, however, at puberty, but, after fifty years of age, again diminish. The blood is richer in solid contents, especially in red corpuscles, in men than in women; the same is true of plethoric and sanguine persons, as compared with those of lymphatic or serous constitution. The quantity of the fatty matter, is more influenced by the diet, than that of the other organic proximate constituents. Exercise in the open air, purifies and oxygenates the blood. This fluid is, of course, profoundly modified in disease.

Hæmorrhage or Loss of Blood.

The escape of blood from its vessels into the surrounding tissues, is named *extravasation*; if into one of the cavities of the body, or externally, it is named *hæmorrhage*. The loss of from four to six pounds of blood, from one or more of the great vessels, will generally prove fatal to an adult; but if the hæmorrhage be slower, much larger quantities may be drawn from the blood-vessels, without a directly fatal issue. Death from sudden hæmorrhage, is caused by the want of sufficient blood to supply the nervous centres, so that fatal *syncope*, *i.e.* fainting, takes place; when death occurs from prolonged hæmorrhage, it is not from a defective supply of nutriment to the tissues generally, but from a slow exhaustion of the nervous and muscular power, affecting the brain, spinal

cord, and heart, due to a deficient supply of nutriment and of oxygen to them, in consequence of the diminution in the number of the red corpuscles.

Everyone should be acquainted with the various forms of accidental hæmorrhage, and their impromptu treatment. If it be *general oozing* from small vessels, which is easily recognised, and if it proceed from a part to which pressure can be applied, a handkerchief closely folded into the form of a pad, and firmly bound over the spot by another handkerchief, will generally suffice to staunch the bleeding for a time; the part should then be kept elevated and at rest. In hæmorrhage from a *vein*, the blood is dark, and the stream flows continuously, welling up over the surface. Moreover, pressure with the finger on the side of the wound further *from* the heart, will almost entirely arrest the bleeding; whilst if pressure be applied on the side of the wound *next* to the heart, the flow of blood becomes more copious. To arrest venous hæmorrhage, a small thick pad should be applied upon the wound, so as to extend a little to the side further from the heart; this should be firmly secured by a handkerchief or bandage; the chief pressure must be made on the side of the wound away from the heart, because that is the direction from which the blood flows. *Arterial* hæmorrhage is known by the blood being bright, and projected in a jet from the wound, sometimes to a considerable distance, usually by jerks, though, if the artery be very small, there are merely slight intermissions in the force of the jet, and, in wounds of very minute arteries, the jet is continuous. Moreover, pressure on the side of the wound further from the heart, has no effect on the stream; but pressure on the side nearer the heart, stops it. To arrest arterial hæmorrhage from a small artery, therefore, a pad of suitable size should be applied upon the wound, and extend also on the side *next* to the heart; it must be, not merely firmly, but *tightly* bound by a handkerchief or suitable bandage. If the artery be large and deep seated, very forcible pressure becomes necessary, and in order to communicate this specially to the artery itself, a small thick and unyielding kind of pad is necessary. This should be made, not by folding a handkerchief, but by rolling it up as tightly as possible, with, or without, some firm substance enclosed within it. Beneath the handkerchief used as a bandage, a short stick may be inserted on the side of the limb opposite to the wound, and then be twisted round, so as to increase the pressure.

These directions apply to veins and arteries situated in the limbs. Upon the head, simple pressure with the thumb or finger, will suffice to stop bleeding from either kind of vessel, because the bones of the cranium afford a perfect means of counter-pressure. Wounds of the large vessels of the neck, require very special management; but, as a general rule, direct pressure with a pad, maintained in its place by the thumb, is the best means to have recourse to, until proper assistance, by forceps and ligature, can be afforded.

In cases of sudden and great loss of blood, living blood, drawn from the veins of another person, has been injected into the veins of those suffering from the hæmorrhage. This

is known as the *transfusion of blood*. Two hundred years ago, Lower (1665) suggested this operation, having found that animals, apparently dead from hæmorrhage, were quickly revived, when blood, taken from another animal, was immediately injected into the veins. As an operation upon the human subject, transfusion was perfected by Dr. Blundell. The blood received into a warmed funnel connected with a proper syringe, is immediately transferred to the veins of the patient, no time being permitted for the occurrence of coagulation. The records of fifteen cases of the saving of life by this operation, have been collected by Bécclard. In experiments on animals, it is better to defibrinate the blood, so as to prevent coagulation; the process of whipping the blood, also, to a certain extent, oxygenates the blood. It has been supposed that the fibrin itself is injurious; but the better oxygenation of the beaten defibrinated blood, may account for its apparent superiority. Arterial blood has been shown to have a greater restorative or stimulating effect, than venous. The serum of the blood is useless for the purposes of transfusion. Water has also no effect, unless it be used warm; it is useful when the blood is loaded with carbonic acid, as in asphyxia, or cold and already thick or tarry, owing to loss of water, as in cholera. Solutions of common salt, or of salts selected so as to imitate those of the blood, yield surprising, but only temporary, restorative results. The blood of one Mammalian species, may be injected, with impunity, into the veins of another species; and, contrary to what was formerly supposed, blood possessing oval red corpuscles, such as the blood of Birds, does not prove fatal when injected into the veins of Mammals, in which the red corpuscles are circular, provided the injected blood be arterial, and not venous, nor previously agitated with carbonic acid (Bischoff). Blood taken from a starving animal, is highly injurious, if injected into the veins of another, causing peculiar symptoms, apparently referrible to the effects of decayed or decomposed animal matter (Bernard). Hence the animal, or person, subjected to transfusion-experiment, or operation, should be in good health, and recently well fed; for then, not only will the loss of blood be better supported, but the blood itself will be newly derived from the food; moreover, owing to the more watery character of the chyle, as compared with the blood, the fibrin in the latter will be diluted, and any injurious influence which this substance might produce, will be diminished.

The accidental injection of *air* with the blood, into the veins, has probably been the cause of the fatal results in some transfusion experiments. Air so injected, or introduced by wounds of the veins in the neck, when it reaches the heart, is speedily fatal, either by mechanically interfering with the functions of the valves, or by chemically failing to excite contraction, like pure blood; or it may induce coagulation, or obstruct the pulmonary capillaries, after it has been driven with the blood, in the state of froth, through the pulmonary arteries.

Vitality of the Blood.

The blood, as it exists in the vessels of a living animal, is not a mere physical and chemical mixture of certain substances adapted to the nutritive wants of the rest of the body; but, with or without the enclosing capillaries, it is an organised fluid tissue, possessing *vitality* like the solid tissues. Its corpuscles are evolved and disintegrated, like the other structural elements of the body. As we shall hereafter see, these bodies are originally developed simultaneously with the earliest vessels of the embryo, and the loss to which they are subject during life, is repaired by corpuscles newly formed in the system. The physiological endowments of these corpuscles, especially of the red ones, are quite peculiar, and are as characteristic as those of any of the structural elements of the solid tissues. With regard to the liquor sanguinis, in which the corpuscles float, it also has vitality, and must be regarded as the liquid, inter-cellular, or inter-nuclear, matrix of a fluid tissue; for it is originally elaborated, with the corpuscles, in the interior of conjoined nucleated cells. The vitality of the liquor sanguinis, is, probably, however, like that of the intra-, or inter-cellular parts of the solid tissues, dependent upon its corpuscles, gymnoplasts, or nuclei, which are its real centres of growth; just as the semi-fluid nervous substance, the somewhat firmer sarcous elements, the areolar fibres, and the yet denser matrix of cartilage, or the solid deposit of osseous tissue, appear to be dependent upon the nuclei proper to those tissues respectively.

The vitality of the blood, is merely a *vegetative life*, its inherent vital properties being strictly nutritive, and including neither contractility nor sensibility. The fluidity of the liquor sanguinis, is an indispensable condition to the life of the whole body, and such vitality as it or the corpuscles

possess, must be constantly exercised in the maintenance of that condition. So, reciprocally, the persistence of the vital properties of the blood, implies, within certain limits, the maintenance of its peculiar fluid state and chemical constitution. Yet, as we shall immediately see, the remarkable change which takes place in one constituent of the liquor sanguinis—viz. : in the *fibrinogen*, or *fibrin*, which, when blood is drawn from the body, solidifies into delicate fibrils, and, entangling the corpuscles, gives rise to the phenomenon known as the *coagulation* of the blood—is, by many eminent physiologists, regarded as a vital act.

The Coagulation of the Blood.

This phenomenon, already elsewhere noticed (Vol. I. p. 65), does not consist of a solidification of all the elements of the blood, but of that of the fibrin alone, of which on an average not above 3 parts exist in 1000 of blood. The effects of this change in so small a quantity of fibrin, are very remarkable. A few minutes after blood is drawn from a vein or artery, it appears to set, or stiffen, into a red jelly-like mass or *clot*; from the surface of this, yellowish transparent drops of fluid very soon exude, which then run together in little pools; the red mass slowly shrinks, forces more and more of the transparent fluid from it, becomes more and more solid, and, at the end of from twenty-four to forty-eight hours, constitutes a clot equal in bulk to about one-third of the total volume of the blood, the rest now consisting of the yellow fluid, which is named the *serum*. This serum contains most of the water, besides the albumen, salts, and extractives of the blood; whilst the clot, coagulum, or crassamentum, is composed of the fibrin, together with the red and white corpuscles. The clot still contains, however, some serum, and, in order to remove this, it is necessary to lift it from that fluid, cut it in pieces, and drain it upon a proper filter.

The composition of the clot and serum, may be inferred from the facts stated in p. 90, Vol. I. When portions of the clot are examined under the microscope, the solidified fibrin is seen in the form of exceedingly minute fibrillæ, not more than the $\frac{1}{300000}$ th or $\frac{1}{500000}$ th of an inch in diameter, nearly straight, subdividing dichotomously, and sometimes assuming the appearance of rows of minute particles. These fibrillæ are most perfect, when the blood coagulates slowly. The red

corpuscles in the clot, are no longer separate from each other, so as to be freely mobile, as in the circulating blood, but have run together in adherent masses or columns, which have been compared to overlapping rows or piles of coins; the white corpuscles are also entangled, but not in groups, though, under certain circumstances, they collect more abundantly in the upper part of the clot.

As freshly drawn blood coagulates, it gives off a vapour known as the *halitus* of the blood. A minute quantity of ammonia escaping in this halitus, is also evolved (Richardson). No carbonic acid escapes, as was once supposed. An *odour*, often characteristic in the case of different animals, is likewise perceptible, not so much during the coagulation of the blood, as before that event takes place, when the blood is hottest. During coagulation, no heat is evolved, the temperature of the blood, indeed, being already lowered, more or less, before this phenomenon begins.

The coagulation of the blood is influenced by many circumstances, which determine its rapidity, and modify the characters of the clot itself, as to form, colour, and consistence.

The external conditions which *accelerate* the formation of the clot, are rest, or, on the contrary, very active stirring, moderate increase of heat, exposure of the blood to air, its slow escape from an artery or vein, its reception into shallow vessels, and contact with rough or multiplied surfaces, or with foreign solid bodies, and, in certain cases, its slight dilution with water. Within the body, the circumstances which favour the coagulation of the blood, are certain enfeebled states of the system, frequent bleedings, laceration of the vessels from which the blood escapes, inflammation of the coats of the vessels, or of the lining membrane of the heart, and so called atheromatous, or other deposits, upon the vessels or upon the valves.

On the other hand, coagulation is *retarded*, or interrupted, by movement, cold, heat beyond a certain temperature, the exclusion of air, as by covering the blood with a stratum of oil, its rapid escape from a vein or artery, its reception into deep vessels, its contact with smooth surfaces, its exemption from the intrusion of foreign solid bodies, and also by the addition of strong solutions of neutral alkaline salts, or of minute quantities of ammonia. Moreover, it is retarded by the admixture of certain vegetable substances containing narcotic and sedative alkaloids, such as opium, hyoscyamus,

belladonna, aconite, and digitalis, and even by strong infusions of tea and coffee. In the case of the addition of strong solutions of neutral salts, and of many other substances, subsequent dilution of the mixed blood, by adding water to it, is followed by a feeble coagulation. The internal conditions which retard coagulation, are certain inflammatory states of the system, perfect smoothness of the interior of the heart and bloodvessels, and, above all, a healthy condition of their lining membrane.

Although *rest*, as when drawn blood is set aside, is favourable to coagulation, and moderate agitation, as when the blood is gently shaken in a bottle, delays this act, it is remarkable that *stirring* blood rapidly with a rod, or *whipping* it with a bundle of sticks or wires, causes the fibrin quickly to coagulate in thready masses on the rod; this is the usual method of defibrinating blood, which afterwards remains fluid, or forms but a very soft imperfect second coagulum. The effect of whipping, depends on the rapid and frequent contact of the multiplied surfaces of the wires with the blood. Again, a *temperature* varying from 100° , or the natural temperature of the blood, up to 120° , accelerates coagulation, but a greater heat retards it; at 150° this property of the fibrin, is said to be permanently destroyed, whilst, above that temperature, the albumen of the blood itself coagulates. When blood is allowed to cool, its coagulation is retarded in proportion to the degree of cold to which it is subjected; at $27\frac{1}{2}^{\circ}$, or $4\frac{1}{2}^{\circ}$ below the freezing point of water, it solidifies; and if it has not been previously allowed to coagulate, and the freezing process is rapidly completed, it will coagulate on being thawed. The coagulating property is, therefore, proportionally, sooner destroyed by an elevation than by a lowering of the temperature of the blood; moreover, frozen blood may be preserved for a long time, and yet retain its power of coagulating when thawed. The influence of *exposure to air*, in accelerating the coagulation of the blood, probably explains the corresponding effects of the slow escape of the blood from the vessels, and of its reception into shallow basins. These conditions do not act by lowering the temperature, for that would retard coagulation, nor by the escape of the halitus merely; but it has been suggested that they operate by favouring the escape of ammonia from the blood. All conditions which facilitate the *escape of vapour* or gas from the blood, certainly favour its coagulation. Thus, coagulation occurs in a vacuum, a fact

which shows that the presence of air is not necessary, a condition too which would favour the escape of ammonia; but it also occurs, and even more quickly, when the blood is subjected to increased atmospheric pressure. Complete exclusion from air, though it retards, does not prevent coagulation, as blood will at last coagulate in closed vessels, and even within the dead body shut up from the air. The rapid escape of blood from its vessels, and its reception into deep glasses or basins, are supposed to retard coagulation, by affording less opportunity of exposure of the blood to the air. Of all the circumstances which hasten the formation of the clot, the multiplication of the points of *contact* with solid bodies seems to be the most potent; the smallest particle of thread suffices to induce rapid coagulation, where, in the absence of any foreign body, a much slower process of clotting would have occurred. Blood received into metal or earthenware utensils, is said to coagulate sooner than when received into glass vessels, perhaps owing to differences of roughness of the surface. The accelerating effect of slight *dilution* and the retarding influence of the addition of *saline solutions*, are not well explained; they may operate, simply by altering the specific gravity, and also the viscosity of the blood. The retardation, or prevention, of coagulation, by the addition of *ammonia*, even if transmitted through the blood, in the form of vapour, the occurrence of coagulation in such blood when the ammonia escapes, and its resumption of the fluid state on the introduction of fresh ammoniacal vapour—phenomena which can be reproduced several times over, in the same blood—are the chief facts adduced, together with the known presence of ammonia in the halitus of the blood, in favour of the hypothesis of Dr. Richardson, that the ammonia is the cause of the fluidity of the blood in the body, and its escape, the immediate occasion of coagulation in drawn blood.

The mode of action of narcotic and sedative *poisons*, is not understood. The more rapid coagulation of the blood in feeble *states of the system*, does not depend upon an increased quantity of the fibrin or coagulating substance, but rather on the dilute or watery condition of the blood. On the other hand, the more slowly coagulating blood of the inflammatory state, is accompanied by an actual increase in the quantity of fibrin, though there appears, possibly from the high specific gravity and richness of the blood, to be a greater resistance to the act of coagulation. The necessity for perfect *smoothness* of the

interior of the heart and bloodvessels, in order to prevent coagulation, may be inferred from the highly polished character of their epithelial lining; the influence of rough surfaces in their interior, in determining coagulation of the blood, is shown by the small coagula formed upon excrescences of the valves of the heart, and by the flakes of fibrin, which collect on atheromatous or calcified portions of vessels, in the rough interior of aneurisms, and at the openings of lacerated vessels, which are so much sooner closed by coagula, than those which are cleanly cut. Coagula have been induced experimentally in animals, in the interior of large vessels, by the passage of needles, wires, or threads into such vessels; when formed in an artery, the coagulum is firm and elongated in the direction of the blood current, whilst, in the veins, the clots are loose and massive. In certain cases, during life, especially during the last hours of life, such coagula may form in the living blood, especially when rough excrescences exist on the valves of the heart. The influence of an *inflamed* condition of the *coats* of the bloodvessels, in causing coagulation of the fibrin, has been referred to the partial loss of vitality, or to the interruption of the vital processes, in the inflamed tissue, by which it is, so far, approximated to the state of inanimate matter. The injection of pus, the pulpy substance of the brain, and other semi-solid matters, into the bloodvessels of an animal, rapidly coagulates the blood, a result probably attributable to the effects of contact with the multiplied surfaces of non-living matter.

Blood confined in a living vein between two ligatures, retains its fluidity for a long time, beginning to coagulate commonly, after from 3 to 5 hours, and sometimes even being only imperfectly clotted at the end of 24 hours, though such blood will coagulate in a few minutes when withdrawn from the living vein. If the vein be dead, although the blood is equally well excluded from the air, coagulation takes place within a quarter of an hour. Experience shows that blood may be retained in occluded vessels, and yet continue fluid for a considerable time, or that blood may be extravasated in the midst of the living tissues, and yet preserve its fluidity for many days, though it will soon coagulate when afterwards withdrawn from the body. From these and other facts, it has been inferred that the *living tissues* possess some special property, by which they maintain, or preserve, the fluidity of the blood; according to one view, they actively prevent its coagulation; according to another,

they operate negatively, by not determining that process, as dead matter would, whether it were an inorganic solid, or a dead animal substance, such as brain substance, dead muscle, or pus. The poisons and the modes of death, which influence the coagulation of the blood, for the most part retard or prevent it. Sudden destruction of the substance of the brain or spinal cord in an animal, causes coagulation of the blood even in the living vessels, in which clots are found after a few minutes. The poison of venomous serpents, appears altogether to destroy the coagulating property of the blood; narcotic poisons, and prussic acid, have the same effect; asphyxia or suffocation, whether from hanging, drowning, or the action of gases unfit to support respiration, also cause the blood to remain fluid after death. In cases of death by lightning, by electric shocks, by blows on the epigastrium, or after a severe chase, the blood has been said not to undergo coagulation; but this seems to be untrue, the blood being often, though not always, found fluid, but after a time undergoing coagulation. In cholera, the coagulation is also postponed.

The *form, consistence, and colour of the clot*, exhibit many varieties. From *healthy* blood, the clot is flat or slightly concave on the upper surface, especially if the blood has been received in a shallow basin, when the clot is soft, and very little serum exudes from it. When an upright vessel is used, the surface of the clot is a little more concave. The consistence of a healthy clot, is firm and uniform; its colour is bright red on the top, from exposure to the air, but dark in its lower portions. In *inflammatory* diseases, especially in pneumonia or inflammation of the lungs, the blood is very rich in fibrin, containing, instead of 3, above 5, often 7, and even as many as 13 parts in 1,000; nevertheless it coagulates slowly, and the coagulum presents a remarkable peculiarity known as the *buffy coat*. Such a coagulum shrinks more than usual, is exceedingly firm, and very concave on its upper surface, forming what is called the "*cup*," which presents a thick layer of a nearly colourless, yellowish, or greenish yellow hue, the so-called *buff* or *buffy coat*. This coat, and the cupped form, are more marked when the blood is received into a narrow and deep basin, than into a shallow one; in the former case, the coagulation is slower, and in the latter quicker, as with healthy blood. The buffy coat is very firm and tough, and, when examined under the microscope, is found to consist of fibrillated fibrin, intermixed with many white corpuscles; from

some cause, the red corpuscles partly subside before the commencement of coagulation, and so escape being entangled in the upper portion of the clot. It was formerly supposed that the slower rate of coagulation of inflammatory blood, accounted for this subsidence of the red corpuscles from the upper strata of the fluid, before coagulation took place; and this view is supported by the fact that the corpuscles, which are heavier than the liquor sanguinis, do subside in blood, the coagulation of which is intentionally retarded by the addition of strong solutions of sulphate of soda or of common salt. But other circumstances probably cooperate to increase the tendency of the corpuscles to settle down. The disposition of the red corpuscles to run together in columns and masses, in blood drawn from the body and left at rest, is increased in the inflammatory state, the corpuscles then running into larger clusters, clinging more firmly together, and even losing their circular form, and becoming elongated. The aggregation of the corpuscles into larger masses, perhaps causes them to subside more rapidly than if they adhered in the usual minute piles or columns; and this, together with the retardation of the coagulating process, may account for the formation of the buffy coat. This unusual aggregation of the corpuscles, also occurs in certain low constitutional states, and, it is said, in plethora; it likewise happens, when the coagulation of the blood is retarded intentionally in experiments. A tendency of the corpuscles to fall to the lower part of a living vein enclosed by ligatures, has been seen in animals. The nature and cause of this tendency of the corpuscles to run together, remains, however, yet unexplained. Their apparent mutual attraction is diminished by the addition of weak saline solutions, and the buffy coat, if the blood be inflammatory, is less distinctly developed, although the period of coagulation is delayed. The addition of any material, which, like mucilage, increases the aggregation of the corpuscles, accelerates the subsidence of the corpuscles, and increases the buffy coat.

Contrasting with the firm, fibrinous, and contracted clot of the blood in inflammation, are the loose, soft coagula, characteristic of the blood of weak, cachectic, and anæmic persons, even though the clot is formed more rapidly. A deficiency of fibrin causes the clot to be soft. During bleeding, the power of coagulation of the blood is gradually modified as the blood flows, the last quantity drawn setting more rapidly, but forming a softer clot. Fragile, almost semi-fluid clots are found in

the blood of those who have died of cholera, from strokes of lightning, or from asphyxia.

That the immediate cause of the coagulation of the blood, is the solidification of the fluid fibrin of the liquor sanguinis, is shown by the existence of the fibrinous fibrillæ, in clotted, but not in fluid blood; by the formation of the buffy coat without any admixture of the red corpuscles, the upper and firmest part of this coat, being nearly pure fibrin; and lastly, by the fact that whipping the blood, which removes the fibrin, prevents any further coagulation, the corpuscles themselves not possessing this power, then remaining free and suspended, or subsiding in the serum, which is likewise no longer coagulable. Experiments also demonstrate this property of the fibrin. Thus, if the coagulation of the blood be retarded by the addition of solutions of neutral salts, the red and white corpuscles have time to subside, and the upper clear fluid, which still contains its fibrin, then undergoes coagulation, the delicate colourless clot exhibiting the characteristic microscopic fibrillæ. Again, by adding a solution of salt or of sugar, to a quantity of frog's blood, the corpuscles of which are very large, the fluid part of the blood, or liquor sanguinis, may be actually filtered from the corpuscles, and will afterwards undergo coagulation.

The cause of the solidification of the fibrin, has been the subject of much speculation and difference of opinion, and is still not satisfactorily understood.

Many living physiologists, agreeing with Harvey, Hunter, and others, maintain, as already stated, that the coagulation of the blood, is a manifestation of vital power in that fluid. Harvey said of the blood, that it was the *primum vivens* and the *ultimum moriens* of the body; whilst Hunter considered the coagulation of the blood as its last act of life. An analogy has been drawn, somewhat vaguely, between the solidification of the fibrin of the blood and muscular contraction, and, perhaps with more justice, between it and the rigor mortis, or rigidity of the muscular tissue after death. Several modern authorities perceive in the fibrillation of the solidifying fibrin, the evidence of an organising plastic process, the feeble efforts of a formative vital energy. Moreover, it is urged that effusions, undoubtedly fibrinous, upon the surfaces of serous membranes, in the interior of the eyeball, between the ends of tendons or other cut surfaces divided subcutaneously, and in other situations, become organised and vascular, and are converted into a low form of areolar or fibrous tissue; and

that not merely fibrin, but even blood clots in the interior of vessels, as in cases of ligature of arteries, or blood extravasated in the midst of the tissues, may also become, under certain circumstances, vascularised, and converted into a definite tissue, in the same way as inflammatory fibrinous exudations are, the blood corpuscles not assisting in the process, but rather delaying it (Hunter, Zwicky, Paget, Hewett).

Notwithstanding the support given to the idea of the coagulation of the blood being a vital act, and of the possession of a vital property of solidification by the fibrin of that fluid, it may be doubted whether this doctrine is correct. There is no real analogy between muscular contractility, which requires peculiarities of structure, and complex statical and dynamical electric conditions, and the simple change of the fibrin of the blood from a fluid to a solid state. If its comparison with the rigor mortis be more exact, the tendency of modern opinion is to regard this phenomenon not as a vital act, but truly as a *rigidity of death*, dependent on chemical changes then ensuing. Again, there is no true resemblance between the minute fibrillæ of solidified fibrin, and any fibrous or other tissue of the body; the former are homogeneous, the latter, indeed, always present differences of parts. Fibrinous deposits or effusions may become the seat of positive organisation, so as ultimately to give rise to a tissue; but then nuclei, or centres of growth, arranged in methodical order, and even cells, appear within it, for the formation of the future tissue elements and the new capillary vessels; these nuclei and cells are supposed to have their origin not in the fibrin, but from the corresponding parts of the surrounding tissues. In cases of so-called organisation of the coagula formed in ligatured arteries, in the interior of inflamed veins, or in other situations amidst the living tissues, it is the surface of the clots next in contact with those living tissues, which first presents appearances of organisation and vascularisation. This suggests the possibility that, subsequently to the effusion of blood, a true plastic exudation may take place around the clot, and may penetrate between the columns of its aggregated corpuscles; in this way, the apparent organisation and vascularisation of a clot, may ultimately be the same process as that of a fibrinous effusion, depending on formative acts on the part of the surrounding cell elements, which give rise to nuclei, cells, or intercellular substance. According to this view, the coagulum of the blood constitutes a sort of nidus for future developmental processes, but is not itself converted

into tissue. The fibrillæ of the coagulated fibrin, may support the effused mass, divide it into areolæ or spaces, and thus favour the penetration of exuded plastic matter, and the penetration of nuclear growths through it. The plastic lymph, though a fibrinous material, may not be identical with the solidified fibrin of the blood, but may be a true protoplasm, more distinctly and positively possessed of organisable tendencies, and thus of a real though low form of nutritive life. If this be so, the strongest argument in favour of the vital character of the coagulation of the fibrin of the blood, is nullified.

Moreover, many facts appear irreconcilable with such a doctrine. Thus, the blood of a horse has been kept in a fluid state, by means of nitre for fifty-seven weeks, and yet speedily coagulated, when sufficiently diluted with water (Gulliver). Frozen blood, as already stated, will coagulate when thawed. If, therefore, coagulation is a vital act, the life of the blood must be admitted to be capable of being "pickled" and "frozen" (Gulliver). It is replied by the vitalists, that the vitality of the fibrin is simply preserved in a dormant condition, by the prevention of spontaneous change or decomposition; just as the dormant vitality of seeds and ova, endures for years, and as that of infusorial animalcules, and even of the highly organised Rotifera, may be restored, after considerable elevation or lowering of the temperature, or may be suspended, and so conserved, by desiccation. But the recovery of animalcules after freezing, is, probably, only apparent, a minute drop of surrounding unfrozen water perhaps defending them from actual congelation; whilst in blood thoroughly frozen, the fibrinous fibrillæ, undergoing no nutritive changes, could hardly escape that event. Furthermore, there is no example of the recovery of life, by any of those minute organised beings, after immersion in so potent a substance as a solution of nitre, which is a well-known solvent of fresh fibrin.

On the supposition that the coagulation of the fibrin, is not a vital, but a *physical* process, it has been maintained that the fibrin is held in a fluid state, in the living blood, by a minute quantity of ammonia, and that the escape of this ammonia is the immediate cause of its coagulation—at least when blood is drawn from the body. The celebrated Robert Boyle (1684) considered that the blood gave out a spirit, and observed that it could be maintained in a fluid state by a salt of ammonia, and that clotting occurred after the removal of this. It was

proved by Haller, that the halitus of the blood is alkaline. Albumen, it is known, is rendered soluble by the fixed alkali, soda, but may be precipitated by the addition of an acid. Lastly, it has been shown, by Richardson, that ammonia is really given off from blood, microscopic crystals of hydrochlorate of ammonia being formed on a piece of glass moistened with a trace of hydrochloric acid, and held over freshly-drawn blood; also that, by the transmission of the ammoniacal vapour from fresh blood, through other fresh blood, the latter may be kept fluid for an unusual time; that air containing the vapour of ammonia, has the same effect, and will, even after coagulation has taken place, restore the condition of fluidity — the clotted and fluid conditions being alternately producible, according as the ammoniacal vapour is passed into the blood, or is permitted to escape from it. The minute proportion of 1 part of ammonia to 3000 of blood, is sufficient to maintain the fluidity of the latter. Finally, nearly all the conditions which appear to favour, or accelerate, the coagulation of freshly-drawn blood, are such as would also facilitate the escape of the volatile alkali from it (Richardson).

Other considerations and facts appear, however, to show that the escape of the ammonia from the blood, which undoubtedly occurs, is not the cause of the solidification of the fibrin, but merely an accompaniment of that change. In the liquefaction of solid fibrin by ammonia, and its alternate re-coagulation and liquefaction by the subsequent subtraction and addition of ammonia, it is not certain whether the fibrin of these secondary and tertiary solidifications, is identical with the fibrin of the primary clot. Many experiments and observations further show that freshly-drawn blood may be placed in such conditions, that its ammonia cannot well escape, and yet coagulation will occur; *e.g.*, when blood is received into a bottle which is quickly stoppered, or when blood rendered fluid by ammonia, coagulates, though tardily, if kept in airtight vessels (Zimmerman); or, again, when blood, subjected to increased barometric pressure, which would check or prevent the escape of ammonia, is found to coagulate even quicker than usual (Colin). Moreover, blood drawn from an animal, and exposed to the air for fifteen minutes, at a temperature of 32° , even though its ammonia had probably escaped, has been found to remain fluid for upwards of five hours, when introduced into the freshly removed heart (Brücke). The blood in a dead body, is usually found coagulated in the heart and the

larger arteries and veins, but fluid in the smaller vessels, although ammonia could apparently escape, or transude, more easily from the latter. This coagulation in the heart and larger vessels, is partly due to post-mortem changes, but, sometimes at least, the clots begin to form during the last moments of life. Again, blood confined between two ligatures in a living vein, retains its fluidity for many hours; but if a piece of glass tube be introduced between the blood and the walls of the vein, coagulation very speedily occurs (Brücke). So, too, when needles, wires, or threads are passed through living vessels, the blood will coagulate in the vessels, though the ammonia could not, by any possibility, escape from the moving blood (Simon and Lister). The coagula thus formed in veins, are large, soft, and dark; whilst those formed in pierced arteries, are small, compact, and pale. In both kinds of vessels, the broadest or attached part, or base of the clot, is directed towards the heart. No escape of ammonia can take place when a clot forms in a ligatured artery, nor in that coagulation of the blood during life, which occurs from the sudden destruction, in animals, of the substance of the nervous centres. Nor can this explain the coagulation produced by the injection of dead brain substance, or of pus, into the blood, nor the fact, that blood enclosed between two ligatures, in a dead vein, speedily coagulates; whilst blood similarly enclosed in a living vein, remains fluid, the facility for the escape of ammonia being apparently, in either case, the same (Astley Cooper, Brücke, Lister).

Indeed, this last-mentioned experiment, added to the well-known circumstances, that blood, extravasated amidst the *living* healthy tissues, remains for a long time fluid, whilst if in contact with inflamed vessels or tissues deficient in vitality, or with the lining membrane of vessels containing morbid deposits, or with dead animal substances out of the body, it quickly coagulates, indicates a striking contrast between the effect of contact of living and dead animal tissues on the blood, the former, in some way, retarding or antagonising the coagulation of that fluid, the latter, in some way, accelerating or determining it (Lister.)

It has been suggested that the immediate cause of the coagulation of the fibrin, may have some relation to the distinction between the crystalloid and the colloid condition of matter (Graham). Fibrin, like all albuminoid bodies, is a colloid substance; and one of the properties of these, is a

proneness to molecular or molar metastases, by which they pass, not only from a pectous to a liquid, but also from a liquid to a pectous state (p. 163). Albumen undergoes this latter change, on the application of heat; casein, on the addition of acid pepsin, or of an acid with heat, and fibrin, still more readily than either, becoming, when left to itself, solidified at moderate temperatures, and, more rapidly, at somewhat higher temperatures. The coagulation of fibrin not being due to any external apparent cause, has been designated *spontaneous*. But this more ready assumption by fibrin, of the pectous condition, can hardly be spontaneous, in the usual sense of that term; unless, indeed, we suppose the vital endowments of this remarkable substance, to be higher even than Hunter believed. Crystallisation is as much spontaneous, in one sense, as coagulation. The latter probably depends upon some definite molecular or molar changes, strictly physical, like any other less rapid effect of colloidal energy, and occurring when the fluid fibrin is removed from the ordinary influence of processes going on in the living vessels and tissues within the body, or when it is subjected to other influences exerted upon it by the dead tissues, or by foreign bodies generally.

The action of these latter may be *catalytic*, or due to contact, and the fact, that rough or multiplied surfaces accelerate coagulation, favours this view. It has been suggested that dead matter may induce a reaction between the solid and fluid constituents of the blood, in which the former, that is the corpuscles, impart to the fibrin of the liquor sanguinis a disposition to coagulate. When, however, no foreign substance is introduced into the blood, the catalytic action has been supposed to be due to the corpuscles themselves, which, as it were, ceasing to undergo their characteristic vital changes, and so, in effect, becoming dead, determine, like other dead animal matter, the solidification of the fibrin (Lister). The influence of the red corpuscles, in producing or accelerating coagulation, is well established; the upper colourless stratum of either inflammatory or diluted blood, in which the corpuscles have subsided, coagulates more slowly than the lower part, in which the corpuscles are present (Gulliver). Chyle, to which a minute portion of blood is added, will coagulate in two or three minutes, though the same, when pure, takes from twenty-five to ninety minutes to coagulate (Schmidt). The fluids of ascites, pleurisy, and pericarditis, that of blisters, and

of other so-called serous exudations, readily coagulate after the addition of a minute quantity of blood, even, it is said, of a few red corpuscles; whilst other portions of those fluids, kept apart, do not. The same effect is produced, however, on the admixture of two such fluid exudations. Fragments of the crystalline lens, the composition of which resembles, or is identical with, the globulin of the red blood corpuscles, and even the crystals of hæmato-globulin obtained from those corpuscles, also induce the formation of a coagulum in these fluids. Hence Schmidt, to whom these latter observations are chiefly due, believes that, within the blood cells, there exists a *fibrinoplastic* substance, and in the liquor sanguinis a *fibrinogenous* substance, and that by the escape of the former and its union with the latter, the act of solidification is effected. But, since dead animal tissues of all kinds, and even clots, or solidified fibrin itself, either fresh, or dried and powdered, produce the same effect, it may be that the action of the corpuscles, in causing coagulation of the fibrin, is not a vital process; and that if, as supposed, their contained globulin escapes, by exosmosis, through their envelopes, into the liquor sanguinis, this is, in reality, a post-mortem event.

Finally, therefore, it is submitted that, out of the body, the solidification of the fibrin, which is the sole cause of the coagulation of *drawn blood*, is due to a mere *physical*, molecular or molar change, resulting in its transformation from a liquid to a pectous state, as is common to colloidal bodies; that this change is permitted, after the life of the blood, or the incessant nutritive mutations which occur in living blood, cease; that it is accelerated, or induced, by the contact of dead matter, either proper, or extraneous, to that fluid, and that it is to be regarded, not as a token of life, but as a sign of death. When coagulation occurs within the body, it is still under conditions indicative of the diminution or cessation of the ordinary vital interchanges of the blood, and so may be equally regarded as a physical process, or, at least, as one of those examples in which the essential cause is physical, though sometimes it may be utilised, and directed to certain formative ends. Lastly, if this view be maintained, the fibrinous fibrillæ of clots formed in the living bloodvessels, or extravasated amongst the tissues, cannot be supposed themselves to be converted, any more than the red corpuscles, into organised tissue elements; but, by their trabecular arrangement, they may facilitate the penetration into such clots, of an organisable blastema, with nuclei or

nucleated gymnoplasmic cells, and intercellular substance, for the production of newly formed tissue.

The formation of an external clot at the mouth of a wounded or divided vessel, is the first step taken by nature, in the effort to close the vessel; to this, succeeds the formation of an internal clot, the base of which, in a divided vessel, corresponds with the wound, the apex extending towards the heart, as far as the nearest branch of any size. From the divided edge of the vessel, a nutritive plasma, or blastema, is poured out, in which nuclei and nucleated cells, probably derived from the surrounding cell elements, appear, and form the future areolar tissue, with its capillary network, which closes the aperture in the vessel. In the case of a completely divided artery, the muscular coat of the vessel contracts, and retracts within the sheath, and so helps its closure: a lacerated or twisted artery retracts even more securely than one cut cleanly across. When an artery is tied, as in surgical operations, its middle and internal coats are cut through by the thread, whilst the outer one is enclosed in the knot; the two former tunics contract, and turn in towards the area of the vessel, and it is upon their cut edges that the primary clot first forms, and from them, that the new tissue, which closes the vessel, is produced; the constricted part of the outer coat, sloughs, and permits the ligature to come away. The artery is closed, and shrinks up to the nearest branch, the primary clot being absorbed: the collateral vessels are greatly increased in diameter, to carry on the circulation beyond the point of ligature. Pressure, by aid of a needle passed through the soft parts upon the side of a divided artery of moderate size, enables its cut end to close: this is now sometimes employed after operations, and is known as *acupressure* (Simpson and others).

SANGUIFICATION.

The occurrence of this process in the economy of the higher animals and of Man, is implied in the popular expression of *making blood*. The corpuscles, both red and white, waste, or become worn out, from the nutritive changes which occur in the solid tissues, and in the blood itself. Their number, especially that of the red ones, certainly increases with a high rate of living, and materially diminishes from hæmorrhage, starvation, or disease. This waste, and loss of number in the corpuscles, must be repaired.

The *white corpuscles* are supposed to be derived from the lymph and chyle corpuscles which enter the blood, and are identical with its white corpuscles, in size, form, structure, and chemical composition. The large number of white

corpuscles found in the blood, three or four hours after complete digestion, their greater abundance in the veins than in the arteries, and especially in the left innominate vein as compared with other veins in the body, are facts which favour this view. No other ordinary source for the production of the white corpuscles of the blood, has been suggested, although it has been supposed that, under certain circumstances, as in local inflammation or excitement, they might possibly arise within the capillaries, by subdivision and growth of the nuclei in the walls of those vessels, and then, becoming detached, be moved on with the blood. Some may also arise within the spleen.

The mode of formation of the blood corpuscles, both white and coloured, in the *embryo* and its membranes, is peculiar, and will be described in the Section on Development. *After birth*, the *red corpuscles*, it is generally believed, are developed from the white ones, however these latter may arise. Many transitional forms have been traced in the blood. In the progress of change in the Mammal, as described by some (Funke, Paget, Kölliker), the contents of the white corpuscle become more fluid and homogeneous, the compound nucleus disappears, the surface becomes smooth, the size diminished, the shape flattened, disc-like and then biconcave, an exceedingly thin envelope forms around them, and they acquire a red colour in their interior. According to others (Wharton Jones, Busk, Huxley), this is true, as regards the nucleated coloured corpuscles of Birds, Reptiles, Amphibia, and Fishes; but in the Mammalian non-nucleated coloured corpuscle, it is the nuclear portion only, of the white corpuscle, which is converted, by the necessary changes, into a red corpuscle. By some, it is thought that the smaller white corpuscles, or the larger ones after subdivision, undergo this transformation, by flattening, disappearance of the nucleus, and acquisition of cruorin; others regard the smaller pale bodies often described in the blood, as if they were wasting, not growing, red corpuscles.

In the Oviparous Vertebrata, therefore, the red-blooded corpuscle is a transformed pale corpuscle; but in the Viviparous Mammalia, including Man, the red corpuscle is the homologue of the nucleus only of the Oviparous blood corpuscle. In both cases, the pale corpuscle is perhaps a naked cell or gymnoplast; but a distinct, though delicate, envelope or cell wall, afterwards appears. The difference between them appears to be, that in the Mammalian red corpuscle, the envelope touches the nucleus, around which there are no cell-contents, or the nucleus disappears in these; whilst in the other Vertebrata, the envelope is at a distance from the nucleus, the cell-contents being abundant. The importance of the nucleus, as a centre of activity, is thus well illustrated.

The *chemical changes* in the corpuscles, are no less remarkable than those which affect their form. Their globulin acquires phosphorus and iron, the former element associated with fat, and the latter with the colouring matter or cruorin. They now also manifest a singular affinity for oxygen. It is not quite certain, in what part of the circulation the change of white into red corpuscles takes place; but it is supposed that this is *completed* during the passage of the venous blood, in which the white corpuscles abound, through the capillaries of the lungs; they are fewer in the arterial blood. The remarkable effects of the respiratory process on the blood, and the strong affinity of the red corpuscles themselves, when fully formed, for oxygen, prove that the oxygenation of the blood, which takes place in the lungs, is accompanied by changes of deep importance in its corpuscles, and favour the idea that it may even be concerned in the conversion of the white corpuscles into red ones.

It has been already stated, that the red corpuscles, after enduring or living a certain time, waste or die. Many writers have supposed that they accumulate in the spleen, becoming impacted, as it were, in the venous sinuses of that organ, and then shrinking and disappearing. By others, again, it is believed that the cruorin, or red colouring matter, is added to the young corpuscles in this organ, perhaps even from the *débris* of those red corpuscles which become stagnated and disintegrated in it.

Besides the corpuscles, however, the intercellular fluid matrix of the blood, or *liquor sanguinis*, is, as we have seen, constantly undergoing loss, in supplying the materials necessary for the maintenance and formation of the great variety of tissues and secretions. Every act of nutrition, like those of secretion, must remove something from, and so far impoverish, the blood. The albumen of the liquor sanguinis, is constantly replenished from that of the lymph and chyle, and, by venous absorption, from the digested food; but it may also contain certain more highly elaborated albuminoid materials, derived from the corpuscles. Some of the substances employed in nutrition, such as the salts and earthy matters, may belong properly to, and proceed from, the liquor sanguinis itself; so also may certain albuminoid matters. But others may merely traverse that fluid, on their way from the blood corpuscles, in which they are finally completed, to the tissues, escaping, through the envelopes of the corpuscles, by dialysis or exos-

mosis, passing across the liquor sanguinis, by liquid diffusion, and then permeating the capillary walls, by dialytic or porous diffusion: so likewise of the fatty matters, which must be immediately added to the blood from the nutrient chyle. Some substances, of a more special kind, may be formed by changes in the corpuscles, and may afterwards traverse the liquor sanguinis to reach the tissues. The elaborative office of the corpuscles, and their influence on the composition and formation of the liquor sanguinis, are undoubted.

The fibrin of the blood, is believed to be derived from the albumen, of which it is said to be a modified, degraded, or more oxidised condition. It has been stated that, on passing a galvanic current through a solution of albumen, a concretion of a substance resembling fibrin, becomes attached to the positive pole (Smee); but this deposit may not be identical with fibrin.

The blood of the hepatic and renal veins, contains only a small quantity of fibrin, and coagulates but imperfectly; hence it has been conjectured that fibrin may be destroyed, or oxidised, in the liver and kidneys. On the other hand, the blood of the splenic vein contains much fibrin, coagulates very firmly, and, even when defibrinated by whipping, will produce a second clot, after long exposure to the air. It is thought also, by some, that the action of the muscles may give rise to an appearance of fibrin in the blood; for on injecting defibrinated blood into the arteries of a recently detached animal's limb, the blood, returning by the veins, is found to contain fibrin, whenever the muscles have been excited to repeated contractions by galvanism.

The amyloid and saccharine matters are probably added to the blood, chiefly from the liver, the inosite from the muscles. The nitrogenous creatin and creatinin, are probably products of the decomposition of albuminoid matter. The colouring matter is possibly, in part, newly formed in the lungs; but previously existing cruorin may perhaps be used again.

The nutritive changes, whether of waste or renovation, in the homogeneous or formless liquor sanguinis, added to those which take place in the organised elements or blood corpuscles, imply a more special, and more complicated, nutritive movement than that which occurs in any *one* of the tissues or glands; for they reciprocate with the metamorphoses of *all* the tissues and glands. The variety of nutritive and secernent changes to which the blood ministers, and in which it itself undergoes

incessant corresponding alterations, is very great, and yet its highly complex, but essential, constitution remains, within certain limits, the same.

The constitution of the blood, is also continually changed, on the one hand, by the accumulation, within it, of its own effete materials, and its reception of those of the disintegrated solid tissues, and, on the other, by its constantly casting out of itself the various products of that decay. In this way, its creatin, creatinin, and urea, and its lactic and carbonic acids, enter, and then escape through the agency of the renal, cutaneous, and respiratory excretions. The quantities of effete extractives and of urea are small, for they are always being carried off; if they accumulate, mischief ensues. Considering that the blood is constantly drawn upon for the supply of nutriment to the rest of the body, that it is intermittently and variously renewed, that it is itself subject to decay in its essential structural and fluid elements, and the seat of constant additions and subtractions, its composition retains a remarkable unity. The complexity of the mutual relations between the blood and the tissues and glands, its renovation from the lymph and chyle, and the rapidity of its purification from the poisonous or injurious chemical products of the disintegration of tissue, by the excretory processes, are very surprising. When imperfectly elaborated, or purified, by the formative, nutritive, and secretory or excretory processes, it becomes unhealthy, and a possible source of disease. Emotional and other disturbances of the nervous centres, may, through their influence over these processes, also render the blood unhealthy or even poisonous. General disorder ensues, and the functions, especially those of the liver, alimentary mucous membranes, kidneys, skin, and mammary glands, are vitiated. Cutaneous and other local diseases arise. Further, the blood may become the vehicle of miasmatic and malarious poisons, or the seat of zymotic decompositions, and so fevers, simple, exanthematous, intermittent or remittent, typhoid or choleraic, may ensue.

THE BLOOD GLANDS.

In Nutrition, certain materials are attracted to, and assimilated by the tissues, from the common nutrient plasma of the blood, and the materials so attracted, are removed from the blood. In the act of secretion, as, for example, in that of saliva and bile by the salivary glands and the liver, various other

materials are separated from the blood. Nutrition and secretion are, indeed, intimately allied, the former being a secretive process, and the latter a nutritive process; hence nutrition is sometimes termed nutrient secretion. Diminished or increased activity, or arrest, of the nutritive processes in certain tissues, such as the nervous or muscular systems, may affect the blood quite as seriously as errors in the secreting processes; and the healthy balance of both functions, is necessary for the preservation of the normal constitution of the blood.

All secreting glands, however, possess special channels, called *ducts*, which open either upon the exterior of the body, as in the case of the cutaneous and mammary glands, or into some internal cavity, as *e.g.* the salivary and gastric glands, and by which the materials separated from the blood, are conveyed away, though some of them may be more or less completely reabsorbed. But in the nutrition of tissues, such as muscle or nerve, the materials separated from the blood, are not carried away by ducts, but remain, for a time, as part of the body, and are only reabsorbed, when they have performed their proper functions, and, in doing so, have undergone further change.

Now, there exist in the Vertebrata generally, and in Man, certain peculiar organs, which, from their compact form, general appearance and relations, and highly vascular character, have been called *glands*; but they have no secreting orifices, channels, or ducts proceeding from them, to open on the surface, or into the cavities, of the body. These organs include the spleen, the supra-renal bodies, the anterior portion of the pituitary body, the thyroid body, and the thymus. From being destitute of ducts, they are named the *ductless glands*; from their obvious connection with the process of sanguification, they are called *blood glands*; and, lastly, from their influence on the blood, being entirely exerted on that fluid within its vessels, they have been termed *vascular glands*. By some, the closed sacs already described (p. 158), as being found in the mucous membrane of the alimentary canal, if not classified as mere dependencies of the lymphatic system, are arranged with the ductless glands.

The organic processes proper to these ductless glands, partake both of the characters of nutrition and secretion. Their substance is nourished like that of a muscle, but each, acting like a gland, separates from the blood something very special. On the other hand, although, like a muscle, and unlike a

gland, they do not yield up their products directly by a duct, yet they doubtless impart to the blood, not merely the effete materials from their waste, but the substances formed by their special elaborative or assimilating power—substances essential to the constitution of the blood itself. They might be termed *nutritive* or *assimilative* glands.

The Spleen.—This organ is a soft, dark, bluish body, attached to the cardiac end of the stomach; it is placed beneath the diaphragm, and is nearly or quite covered by the lower ribs. Its shape is a flattened oval, convex and smooth on its left surface, and concave on the right surface, which is applied to the great *cul-de-sac* of the stomach. Along this surface is a vertical fissure, named the hilus, sometimes notched in front, at which the bloodvessels, lymphatics, and nerves pass in or out. By these last-named parts, by a peritonæal duplication, named the *gastro-splenic omentum*, and by a reflection of the peritonæum from the spleen on to the diaphragm, named the suspensory ligament, this organ is held in its place.

The size and weight of the spleen, vary more than those of any other solid organ in the body, not only in different persons, but at different times in the same individual. This is chiefly owing to changes in the quantity of blood it contains. It usually measures about 5 inches in length, $3\frac{1}{2}$ from front to back, and $1\frac{1}{2}$ from side to side; its average weight is about 6 ounces, but it may vary from 4 to 10 ounces. Up to the age of forty, its proportionate weight to that of the body, is as 1 to 350; after that age, the ratio diminishes gradually to 1 to 700. In ague and other fevers, the spleen becomes enlarged by increase of substance, as well as by distension with blood, sometimes weighing 20 lbs. In certain diseased conditions of this organ, it has weighed 40 lbs.; on the other hand, it has been reduced to $\frac{1}{4}$ of an ounce in weight. Its specific gravity is about 1060.

Within the peritonæal *serous* covering, the spleen has a proper, strong, *fibro-elastic* coat, which is prolonged, at the hilus, into the interior of the organ, forming elastic sheaths around the bloodvessels, lymphatics, and nerves. Crossing in every direction between these sheaths and the inner surface of the elastic coat, are numerous slender elastic bands, named *trabeculæ* (*trabs*, a beam). In the spaces, or *loculi*, formed between these trabeculæ, outside the vessels, is contained the so-called *splenic pulp*. This is a soft, bluish-red or brownish

mass, which may be pressed out from the intertrabecular spaces, and which becomes of a brighter red when exposed to the air.

The proper coat, the sheaths of the vessels, and the trabeculae, consist of white fibrous and areolar tissues, mixed with elastic fibres, and contain, especially in animals, pale, fusiform, unstriped muscular fibre-cells. The splenic pulp consists of a colourless, granular parenchyma, mixed with numerous coloured cells, with red blood corpuscles of various size, shape, and state of aggregation. The colourless parenchyma is composed of round, oval, and fusiform nucleated cells, of nuclei, and of a granular matrix; it somewhat resembles the contents of the sacs of the solitary and agminated intestinal glands. The coloured cells, or altered red blood corpuscles of the splenic pulp, are peculiar to this organ. Some closely resemble the ordinary red blood corpuscles; others, however, are smaller, and of a bright golden colour, brown, or black; sometimes their contained pigment is gathered into a rod-shaped mass, or into some crystalline form, or is broken up into minute granules. Frequently they present the unique condition of agglomeration into little clusters or heaps, which are sometimes free, but sometimes enclosed in a delicate membrane, or encysted, so as to appear like large compound cells, containing from two or three, to as many as twenty altered blood corpuscles.

Embedded in the splenic pulp, are numerous whitish vesicular bodies, measuring from $\frac{1}{6}$ th to $\frac{1}{3}$ rd of a line in width, named the *Malpighian corpuscles* of the spleen; they are attached, in clusters, to the small arteries, and are supported on the trabeculae, so as to appear like sessile buds or fruit upon a stem. Their envelope is partly derived from the fibrous coat of the artery, and partly from the outer harder layers of their contents. Their cavities have no communication with the bloodvessels on which they rest. Smaller bodies found in the spleen, are said to be Malpighian corpuscles in an immature state. They are composed of an extremely delicate, imperfectly fibrous, envelope, enclosing granular, nuclear, and nucleated-cell elements, like those of the splenic pulp itself.

The *splenic arteries*, entering at the hilus, ramify through the spleen by rapid subdivisions, without anastomoses, after the manner of the branches of a tree; many quickly divide into a coarse *capillary* network, which as speedily ends in the minute veins. The capillaries are most abundant in the splenic pulp,

and also on the surface, and in the interior, of the Malpighian corpuscles. The smallest *veins* chiefly end, almost immediately, in larger ones, which form close plexuses and venous diverticula between the trabeculæ. Recent researches show, that whilst some of the arteries end in capillaries, from which veins arise in the usual manner, other of these vessels end in veins which suddenly enlarge, and, lastly, others even terminate in *lacunæ*, or spaces destitute of distinct walls, but bounded only by the elements of the pulp (Gray, Billroth). The interior of some of the veins, presents a closely dotted appearance, from the numerous openings of little venules or diverticula around them. In the blood of the veins, splenic cells, altered blood corpuscles, and clustered blood corpuscles, are sometimes found, as from mutual extra- and intra-vasation. The blood of the splenic veins contains, however, fewer red corpuscles, but more fibrin, than other venous blood. On escaping from the hilus, the venous trunks unite to form the splenic vein, which, like the other tributaries of the portal system, is destitute of valves; some of the veins of the spleen pass on to the stomach, and join with its veins. The *lymphatics* of the spleen, divided, as usual, into a superficial and deep set, are by no means numerous. The mode of origin of the deep set, is unknown. It has been supposed that the cavities of the Malpighian bodies, communicate directly with the lymphatics, but this has not been proved. The spleen is supplied with comparatively few *nerves*, which are derived from the sympathetic system.

The splenic pulp, with its granules, nuclei, and nucleated cells, must be the seat of rapid nutritive and formative processes. The bulk of this organ, increases in a marked manner during, and especially towards the end of, the process of digestion; an enlargement due, not only to an increase in the quantity of blood contained in the splenic vessels at that period, but also to a simultaneous increase in the quantity of all the microscopic elements of the pulp itself. Even the Malpighian corpuscles increase in size, and, it is said, in number, after the digestive process is completed. Their diminution in both respects, in states of exhaustion and innutrition preceding death, may account for their existence in Man having been denied. In starving animals, the Malpighian bodies are certainly few and small, or they may even disappear; whereas they become larger and more abundant, in those which are well fed. The coloured cells, or altered red blood corpuscles, are

likewise increased in number in highly nourished conditions of the body.

Since the colourless nuclei and nucleated cells of the spleen, bear some resemblance to lymph-corpuscles in an early stage of development, and since, in certain conditions, such corpuscles, then considered as nascent white blood corpuscles, are found in large numbers in the blood of the minute veins and larger venous trunks, the spleen has been regarded, by Hewson and others, as one of the seats of formation of the white corpuscles of the blood, probably by the successive subdivision of old cells, thus acting, as it were, as a large *lymph-gland*, directly connected with the venous system. In certain cases of enlargement of the spleen, white corpuscles are found in extraordinary number in the blood of the splenic vein, so as even to alter its colour, and the number of these white corpuscles in the blood, generally increases to such an extent, that their proportion to the red corpuscles, may be as high as 1 to 10. This condition has been named *leucæmia* or *leucocythæmia*, meaning white blood.

It has also been supposed (Kölliker, Funke, Billroth) that the spleen may be the seat of formation, in some yet undetermined way, of commencing red corpuscles. The small bright yellow corpuscles, enclosed in larger cells, may undoubtedly be traced in the spleen, through a series of intermediate phases, into the ordinary flattened disc-like red corpuscle; but that these appearances indicate an upward development, is doubtful. On the contrary, it is suggested that the red blood corpuscles, having for a time performed their functions in the circulation, and having lived, as it were, their natural life, may really undergo disintegration and destruction in the spleen (Kölliker). This hypothesis requires another mode of interpreting the microscopic appearances just described, as to the alteration, agglomeration, and encystment of the red blood corpuscles in this organ. Since clusters of altered red corpuscles, are found in the splenic veins, it has been inferred that they proceed from the interior of the vessels, and are extravasated into the pulp when sections are made of this organ; but if the undefined spaces or lacunæ, described by Gray and Billroth, exist, the presence of these altered blood cells in both the pulp and the veins, and likewise the passage of the white nuclear and nucleated elements of the splenic pulp into the veins, would be easily explained. In support of the view that the red corpuscles decay in the spleen, it is said that when the spleen is

removed in frogs, these corpuscles become heaped or agglomerated in the blood itself (Moleschott). Moreover, as the quantity of fibrin in the blood of the splenic vein, is greater than in any other part of the venous system, it has been suggested that this excess of fibrin, is derived from the partial oxidation of the globulin of the red corpuscles, which are relatively diminished in number in the splenic vein. The oxygen necessary for this change, is that belonging to the corpuscles (Béclard).

Active and important chemical changes, however, must occur in the capillaries and in the pulp of the spleen; but these are not yet understood. The chemical composition of the pulp, which resembles closely that of the blood, is very complex. In every 1000 parts, there are 750 of water, 242 of organic, and 8 of saline and earthy matters. The organic substances consist chiefly of albumen, or some albuminoid body; besides this, there are traces of fat, and certain quantities of pigment like that of the blood, with smaller quantities of inosite, sarcin, leucin, tyrosin, xanthin, and even of uric acid. Soda and iron are the chief inorganic substances.

The variable size of the spleen under different conditions in the same person, has attracted much notice. It reaches its largest dimensions, five hours after a meal, *i.e.*, near the termination of the process of chymification; seven hours later, provided no food has been taken, it is reduced to its smallest size, and is then also most deficient in blood. The elasticity of the whole fibrous framework of the spleen, including its proper coat, the sheaths of the vessels and the trabeculæ, and also the large size of its veins and the absence of valves in them, facilitate the distension of this organ with blood during the turgid condition of the vascular system, which results from the venous and lacteal absorption of the products of digestion. The resiliency of those elastic tissues, will also favour the diminution of the organ in an opposite condition of the system. But the pale muscular fibres of the spleen, which exist in abundance in the larger animals, and in smaller number in Man, may, by alternate conditions of relaxation and contraction under the influence of the sympathetic system, or of some direct stimulus, materially assist in these remarkable changes of size. Electrical currents passed through the spleen, cause that organ to contract. It has long been supposed that the alternate enlargement and diminution of the spleen, serve a mechanical purpose, and that this organ acts as a diverticulum

to the entire portal venous system, or to the vessels of the stomach and duodenum, in connection with certain changes in the circulation, dependent on digestion. The small size of the spleen during that process, is attributed to the bloodvessels of the stomach and duodenum, being at that period distended; whilst, when digestion is completed, those vessels diminish in size, and the spleen enlarges. The spleen is certainly quickly reduced in size, when the portal venous system is unloaded by hæmorrhage or by purgatives, and it becomes enlarged in obstructive diseases of the liver and heart; but the idea of its serving specially as a diverticulum, is too mechanical, and but partially expresses its true function. A mere plexus of bloodvessels would have sufficed for such a purpose, without the co-operation of a peculiar parenchyma, like the splenic pulp; moreover, as already stated, not merely are the bloodvessels of the spleen, distended during its periodic enlargement, but the splenic pulp itself, and even the little Malpighian bodies, are obviously increased in volume.

Notwithstanding much that is obscure in the history of this organ, it would seem, from the abundance and character of its microscopic elements, its chemical composition, its large supply of bloodvessels, and the peculiar relation of these to the pulp, that the spleen probably has for its office, as an assimilative or nutritive gland, the elaboration of the albuminoid constituents of the blood, and perhaps, as Hewson long ago suggested, the formation, like the lymphatic glands, of the germs of the white and red blood corpuscles. The supposition that it is also the seat of a degeneration of the red corpuscles, is no contradiction to such a view. Some of the materials of the old corpuscles, as, *e.g.*, the pigment, may be used up again in the formation of new ones; for, like all ductless glands, the spleen, whilst, on the one hand, it abstracts materials from the blood, by special nutritive processes, on the other, it returns to that fluid, in some altered condition, all that it has so attracted from it.

The *supra-renal bodies* or *capsules*.—These organs, two in number, one on each side of the body, are small, flat, triangular, yellowish masses, placed on the summit of the corresponding kidneys, which they surmount like a cocked hat. Each measures about $1\frac{1}{2}$ inch in width and 2 or 3 lines in thickness, and weighs nearly 2 drachms. They consist of an outer deep-yellow, firm, cortical portion, and of an inner dark, soft, medullary part, the whole organ being invested by a proper

areolar coat, which sends prolongations into its interior. The *cortical* part presents numerous oval loculi, or spaces, in the areolar framework, placed end to end in little rows or columns, and arranged perpendicularly to the surface. These loculi were formerly thought to be oval or tubular closed vesicles, with distinct walls; but they are merely interspaces in the areolar framework of the organ. They contain a granular plasma, composed of an abundance of granules, with few or many fat particles, nuclei, and nucleated cells; towards the centre of the organ, the cells are larger, and less regularly arranged, so that the columnar appearance is there lost. The *medullary*, or softer central portion, is composed of a delicate filamentous tissue, connected with the areolar tunic and framework of the cortical substance, and having in its interspaces also, besides bloodvessels, a granular plasma, containing nuclei and certain cells, the latter resembling the ganglionic cells of grey nervous substance (Leydig, Kölliker). The *arteries*, numerous and small, reach the supra-renal bodies at many points of their surface, and ramify between the rows of loculi, ending in capillary networks around them. The *veins*, also numerous, are collected into a plexus in the centre of the organ, where a venous sinus, sometimes taken for a gland cavity, is found. The *lymphatics* are said to be not very numerous. The *nerves*, however, are very large, and are derived chiefly from the sympathetic, but also in part from fibres of the pneumo-gastric and phrenic nerves.

From the quantity of blood received by the supra-renal bodies, and from the number and character of their microscopic elements, it is evident that the nutritive processes which take place within them, are very active. Probably, like the spleen, they modify the blood passing through them, by subtracting from it, and returning to it, certain materials in an altered form; but their precise function is unknown, whether this be entirely elaborative, or partly destructive. A curious bronzed colour of parts of the skin, has been frequently seen in disease of the supra-renal capsules (Addison, Hutchinson); but cases of similar cutaneous bronzing, have been noted, in which the capsules were healthy (Parkes, Harley); moreover, these organs have been found diseased without bronzing of the skin (Kirkes, Day, Hutchinson). From the numerous cells, like ganglionic cells, in the medullary portion of these bodies, it has been suggested that this part may constitute a nervous apparatus, or be nutritively connected with the nervous system.

The Pituitary Body.—The posterior lobe of this body (vol. i. p. 305) consists of true nervous substance; but its anterior lobe is composed of an areolar framework, forming loculi or spaces, which contain a granular plasma, nuclei, and nucleated cells of various forms, a structure somewhat, though not precisely, like that of the cortical part of the supra-renal capsules, or the vesicles of the thyroid body. It may, therefore, be temporarily classified with the ductless glands, though not from any established identity or similarity of function, which is wholly unknown.

The Thyroid Body.—This body, commonly named the thyroid gland, is a soft, reddish-brown, vascular organ, placed upon the front and sides of the upper part of the trachea, and reaching upwards to the sides of the larynx, to which it is suspended. It is formed of two lateral, somewhat pyriform lobes, joined together, at their lower and larger ends, by a transverse part, named the *isthmus*. The lobes are about 2 inches long, and measure $\frac{3}{4}$ of an inch in their thickest part. The thyroid body varies in weight from 1 to 2 ounces; it is larger in the female than in the male.

The thyroid body differs in structure from the other ductless glands, inasmuch as its proper tunic and framework of areolar tissue, forms loculi, in which are embedded multitudes of rounded closed vesicles, bounded by a distinct membrana propria, and lined by an epithelium. The vesicles, which measure from $\frac{1}{2000}$ th to $\frac{1}{85}$ th of an inch in diameter, contain a viscid, clear, albuminous fluid, in which are found nuclei and cells resembling the uniform epithelial-like layer. The arteries, four in number, and of considerable size, end, between and upon the walls of the vesicles, in a close capillary network, which empties itself into the *veins*. The *lymphatics* are numerous and large; their relations to the structural elements of the thyroid body, are unknown; but it is supposed, from their relative size and abundance, that they are more concerned in returning the contents of the thyroid vesicles to the blood, than the lymphatics of the supra-renal bodies, or spleen, are, in regard to those organs.

Enlargement of the thyroid body constitutes the disease known as *goître*, in which the condition of white blood, leucocythæmia, or leucæmia, is often induced. In such cases, the nucleated cells of the thyroid body, and their contained nuclei, are smaller than usual, and, a fact of much interest, the white corpuscles of the blood are not only more numerous

than in health, but are also unusually small. This so far favours the view, that the thyroid body may aid in the formation of the morphological constituents of the blood.

The thyroid body may also influence, like the other ductless glands, the chemical composition of the circulating fluid. The chief constituent of the glairy fluid of the thyroid vesicles, is of an albuminoid nature; but, unlike the splenic pulp, it contains a noticeable quantity of fatty matter. Its extractives and salts differ in no important particular, from those of the blood.

Some physiologists have supposed that the thyroid body acts mechanically, as an occasional diverticulum for the blood concerned in the cerebral circulation; but the evidence of this, is even less than that adduced on behalf of a similar hypothesis concerning the spleen and the portal circulation.

The *goitrous enlargement* of the thyroid body, which produces such unsightly disfigurement of the neck, is most frequently met with in females. It prevails in particular countries, and in particular districts of those countries. Thus, it is met with chiefly in the north of Italy, and in certain cantons of Switzerland, most markedly in the canton of the Valais. In other European countries, it is met with much less frequently; but still asserts a preference for particular districts. In England, it is most common in Derbyshire, and hence its popular name, the Derbyshire neck; but it is observed in many other scattered localities. In spite of careful investigations, involving researches into the climate, solar influence, atmospheric peculiarities, rain-fall, soil, and drinking-water of those districts, and into the manifold conditions of existence of the people, the true cause of goître has not yet been inductively ascertained. It is more common in the country than in towns, and is almost entirely confined to hilly and mountainous districts, being more particularly observed in the valleys of those districts; but it is not prevalent in all elevated or mountainous regions. It has been variously attributed to the deficiency of oxygen in the higher levels of the atmosphere; to the want of solar light in valleys, especially since, as is alleged, it prevails more on the southern, and comparatively sunless, sides of such valleys; to the habitual use of drinking water derived from the melting of glaciers or of snow, and therefore almost entirely destitute of saline and earthy salts; and, again, on the contrary, to the presence of lime, but particularly of magnesia, in such water, derived from the limestone or magnesian limestone, often found in districts in which goître is common. Lastly, its special prevalence amongst females, has been assigned to the custom, in hilly districts, of carrying water, or other heavy substances, on the head, by which it is alleged that the muscles of the neck compress the veins, and so cause congestion, and ultimate enlargement of the thyroid body.

In the canton of the Valais, where goître prevails in its most intense form, it is often associated with an arrest of development of the whole frame, especially of the skull and brain, which constitutes the condition known as *Cretinism*. The Crétin may, indeed, be said to be a small

idiotic human being, distinguished from ordinary idiots, by the thyroid body being enlarged or goitrous. But in the Crétin districts, persons of full stature, of duly proportioned cranial and cerebral development, and of ordinary intellectual capacity, are seen with goîtres larger even than those found in Cretins themselves.

The *thymus body*, or *thymus gland*.—This ductless gland is a temporary organ in the animal economy. Present in the embryo, it attains its largest relative size to the body in the infant, and seems to be most active in function a short time after birth, growing up to that period even faster than the body. It then continues to grow, so as to keep pace with the rest of the body, up to the age of two years; but soon, it no longer increases with the body, and, at about twelve years of age, is usually changed into a fatty mass; according to Friedleben, it may grow a little after the second year, and not become fatty until after puberty. Finally, especially in thin persons, it gradually wastes, so as to leave nothing but a mere vestige behind.

In its most complete condition, it forms a double organ, composed of two lateral irregular *lobes*, joined by a central mass, and situated partly in the lower region of the neck and partly in the thorax, lying upon the trachea and the great bloodvessels. It measures, at birth, about 2 inches in length, and weighs half an ounce. It is a soft, pinkish-grey body, consisting on each side of a string of compressed lobules, connected together by an elongated part, like a cord. A strong areolar coat encloses, and connects, the various lobules, and sends intervening coverings between their ultimate subdivisions. The lobules, or acini, are composed of a soft milk-white parenchyma, consisting of granular matter, nuclei, and nucleated cells; the central part of each lobule, is so soft or fluid, that, when opened, a cavity is found, which extends into the secondary lobules, of which the primary ones are composed. The cord which connects the lobules together, contains the same parenchymatous substance, and is likewise soft or fluid in the centre, so as to form a cavity, called the *reservoir of the thymus*; this communicates with the soft cavities of all the lobules, and also with certain small sacculi situated in its walls. Each lateral half of the thymus, has its proper reservoir, the two sometimes communicating through the central transverse mass. The cavities within the lobules and connecting cord, are not lined by a distinct limitary membrane and epithelium; the fluid within them, is milky white, and

resembles chyle. It contains nuclei and nucleated cells, similar to those of the white parenchyma itself. Many of these closely resemble the developing lymph-corpuscles found in the loculi of the lymphatic glands, and, therefore, also the white corpuscles of the blood. No minute fatty molecules, similar to those forming the "molecular basis" of the chyle, are found, however, in the white fluid of the thymus. To chemical analysis, this body yields about 20 per cent. of solid matter, chiefly albumen, some gelatin, only a little fatty matter, and traces of sugar, leucin, sarcin, xanthin, salts of formic, acetic, succinic, and lactic acids, chloride of potassium, and alkaline and earthy phosphates. The bloodvessels of the thymus are large and numerous; the *arteries* penetrate to the central cavity, and thence ramify towards the surface of the lobules; the *capillaries* traverse the soft white parenchyma in all directions, the chief terminal plexuses being near the surface of the lobules; the *veins* are large and, what is unusual, do not accompany the arteries. The *lymphatics* are also numerous and of great size, terminating, some in the thoracic duct, others in the right lymphatic duct, and others directly in the neighbouring large veins. It is supposed that the lymphatics assist in conveying the contents of the cavities of the thymus into the blood; but their direct communication with those cavities has not been demonstrated. The *nerves* are small, and are derived from the pneumogastric nerve, and the sympathetic system.

The office of the thymus, would seem to be, to prepare an *albuminoid* pabulum, fitted for the formation and maintenance of the blood, exactly at that period of life when growth is relatively most rapid, *i.e.*, in the earliest years of infancy. It is possible, moreover, that its nuclei and nucleated cells, especially those which resemble the lymph-corpuscles, are the germs of future white blood corpuscles, a view especially urged by Hewson. The almost complete absence of fatty matter, hydrocarbons, or carbohydrates, from the thymus, as well as from the thyroid body and spleen, would seem opposed to the idea, that any of these organs stored up such substances for the direct purposes of combustion. Yet it has been conjectured that the fluid of the thymus, forms a reserve of material suited for oxidation in the respiratory process, at a time when such matters, derivable from the waste of muscular tissue, are by no means abundant (Simon). Later, however, in fully nourished children, the thymus becomes quite fatty, its nucleated cells

being converted into adipose cells, which might then yield their fatty combustible matter to the blood. In the hibernating Mammalia also, this organ continues to grow more rapidly than the body, up to the adult period of life, and, when thus persistent, contains much adipose matter. This is also said to be the case in most Reptiles. It was at one time held, that the thymus body acted as a diverticulum, in regard to the pulmonary circulation, in the child.

The *closed sacs* of the *tongue*, *tonsils*, *pharynx*, *stomach*, and *intestinal canal*.—These, as elsewhere described (p. 158), whether solitary or clustered, may be regarded as minute representatives of the larger ductless glands, to which in their closed form, their vascularity, and their albuminoid, granular, nuclear, and nucleated cell-contents they bear a certain generic resemblance. They might, indeed, be compared to the Malpighian bodies of the spleen; but they differ from the vesicles of the thyroid body, in having no distinct cavity lined by an epithelium. They might be said to stand in the same relation to the larger ductless glands, that the small and simple tubular glands of the stomach and intestine, do to the large secreting glands, with extensive excretory ducts.

The *ductless* or *vascular glands* considered generally.—Before the structure of these organs was less understood than it is at present, they were sometimes supposed to possess parts analogous to the terminal acini, vesicles, or dilated ends of the ducts of true secreting glands; and the absence of the ducts themselves, was said to form the most marked distinction between them and these glands. But the thyroid body alone has distinct vesicles, limited by a *membrana propria* and an epithelium, and so far approximating to the characters exhibited by the commencing ducts of a secreting gland. In the spleen, and even in the supra-renal bodies, the inter-trabecular areolæ, and the columnar loculi, are not so surrounded, but are mere interspaces in an areolar framework. The minute encapsuled Malpighian bodies of the spleen, and likewise the closed sacs of the alimentary canal, have no lining epithelium or true basement membrane. The branching sacculated canals, and secondary cavities, or acini of the thymus, cannot be compared to true glandular structures, for they also are destitute of a lining membrane and epithelium. Indeed these ductless glands, instead of resembling the secreting glands with ducts, possess characters approximating them rather to the lymphatic glands, with their numerous loculi and albu-

minoid corpuscular contents; but they differ in this, that their cavities do not open directly into the lymphatic vessels.

Considered generally, their proper parenchyma, with its granular plasma, nuclei, and nucleated cells in various stages of growth, constitutes their most important and characteristic anatomical element. The rest of their structure, is either the framework of the organ, or consists of the bloodvessels, lymphatics, and nerves.

The physiological influence of these organs in the economy, must be exercised on the blood, and must be exerted, especially through a nutritive process, by the nuclear and nucleated cell-like constituents. The blood entering such an organ, yields to it, by exudation through the walls of the capillaries, a common plasma, from which, by a nutritive process dependent on the special attractive, selective, and assimilative powers of the microscopic elements, certain special materials are separated. The residue of the plasma, re-enters the circulation, either directly through venous, or indirectly through lymphatic absorption, as in every instance of simple nutrition. Hence, in the first place, the blood which passes through these organs, must be modified, as in all nutrition, by the abstraction of certain of its constituents; and the effect is peculiar in each organ.

But, secondly, the proper substance of these ductless glands, cannot remain unchanged and inactive, subject to no further metamorphoses, and productive of no special influence upon, or service in, the economy. On the contrary, it would seem certain, that something must also be added, by their agency, to the blood as it passes through them. The materials attracted from the blood by their proper substance, and elaborated within them by a sort of nutrient secretive act, are returned, more or less altered, into the blood current. This may chiefly be accomplished by solution and venous absorption in the spleen, supra-renal bodies, and thyroid body, or by lymphatic absorption in the thymus and closed sacs of the alimentary mucous membrane, or by occasional opening of the loculi into the veins, as in the spleen, or into the lymphatics, as conjectured by some to be the case in the thymus.

By both subtraction and addition of material, the blood must be specially modified, as it passes through those organs, which, from their various actions, contribute, therefore, to the elaboration and maintenance of the complex chemical constitution of the blood. It is for the preparation of the *albuminoid*

constituents of the blood, that these organs are destined, and not for the formation of fatty matter, which is so scanty in their composition. Their action upon the colouring matters, which are also albuminoid, may be, in the case of the spleen and supra-renal bodies, to decompose or re-compose those peculiar substances. Moreover, from the resemblance of the microscopical elements of their abundant and characteristic parenchyma, to the white blood corpuscles, they are probably concerned in the formation of those bodies, and therefore of the future red corpuscles, assimilating the nutrient plasma of the blood into distinct morphological elements, just as the lymphatic glands and vessels develop a corpusculated fluid in their interior. Hence, both chemically and morphologically, the blood glands are believed to contribute to the important process of sanguification. The products of nutrient secretion, formed by these organs, all enter the systemic veins, excepting those elaborated by the spleen, which first enter the portal blood, and so pass through the liver, before they reach the right side of the heart, to be sent to the lungs.

It is remarkable that all the large ductless glands are present and active during embryonic life, and also in the most active period of growth after birth. The supra-renal bodies, at first, in the embryo, much larger than the kidneys, are, in the adult, only $\frac{1}{28}$ th part of the weight of those glands. The thymus especially ceases, after birth, to grow in proportion to the rest of the body, and then gradually wastes; a positive relation has been observed, in young animals, between its size and the state of their nutrition. The thyroid body and the pituitary body are also larger proportionally in the embryo and the infant, than in the adult; but they continue to be present throughout life. At birth, the weight of the thyroid body, as compared with that of the body generally, is as 1 to 250 or 1 to 400; but it soon ceases to enlarge with the body, for, after three weeks, the proportions are as 1 to 1166, and in the adult only as 1 to 1800 (Krause). The spleen, however, enlarges with the body, and maintains its proportionate size; but it is undoubtedly largest in the most active period of life, about early manhood. As to the closed sacs of the tonsils, tongue, pharynx, and solitary and agminated glands of the stomach and intestine, they exhibit a continuous development with the rest of the body, and are permanent structures.

Finally, it would seem, that, whatever may be the general or

special uses of the ductless glands, some of them, at least, are not absolutely essential to life. The thymus, though very large in the early period of development and growth, ultimately disappears as a distinct organ. The thyroid body may be totally altered by disease, becoming cystic, indurated, or filled with earthy deposits, without serious detriment to the health. The spleen has been extirpated from animals, without any obvious ill consequences, and, it is said, in a few cases, even from the human body. In certain animals, the spleen is multiple, minute detached spleens, named splenculi, existing near the principal organ. When the latter is removed, the splenculi become enlarged, and so supply, physiologically, the place of the extirpated spleen. In other cases, the lymphatic glands of the neck and axilla, have become increased in size; and, on the whole, the result of such experiments, would seem to show, not the want of importance of the spleen, but that its functions may be performed, as it were vicariously, by other organs of the body. The same may be true in cases in which the thyroid body is diseased. It is said, however, that in animals, after removal of the spleen, the quantity of iron in the blood, is diminished, and that the appetite becomes voracious, and the temper fierce. Removal of the supra-renal bodies is fatal; according to some, directly, owing to the retention of some poisonous substance in the blood; according to others, indirectly, as a consequence of the incidental injury to the nerves and other neighbouring parts (Harley).

THE LIVER CONSIDERED AS A BLOOD GLAND. GLYCOGENIC
FUNCTION OF THE LIVER.

The action of the ductless or nutritive glands, viz. that of extracting material from the blood, elaborating it, and, instead of eliminating it by ducts, returning it into the blood, by means of venous or lymphatic absorption, is, to a certain extent, imitated by the liver, the largest secreting gland in the body. In the embryo, the liver is, indeed, a true *blood gland*, blood corpuscles even being developed in its capillary network. But probably then, and certainly after birth, the hepatic nucleated cells, which secrete the bile, like the special parenchyma of the ductless glands, attract and assimilate material from the blood, and form a peculiar substance, which is not discharged by the bileducts, but enters the blood either

through the veins or the lymphatics; most probably, however, through the former. But this substance, is not albuminoid, like the supposed products of the assimilative action of the ductless glands; it is amyloid, forming an *animal starch*, closely resembling the amylaceous substances developed so abundantly in the Vegetable Kingdom. By Claude Bernard, its discoverer, it was named *glycogène*, from its yielding sugar when mixed with ferments; it has also been called *hepatine* (Pavy), and *zo-amyline* (Rouget). It is obtained by bruising the substance of the liver in water, boiling the fluid to coagulate the albumen, filtering through animal charcoal, and then precipitating the substance sought for, by means of pure acetic acid, or alcohol. It is white, tasteless, flocculent, and readily soluble in pure water; with iodine, it forms a reddish violet compound, the colour of which disappears at a temperature of 176° , but returns on cooling. It does not reduce the salts of copper. Minute granules, apparently covered with an albuminous fibrin, are found in the hepatic cells; these are not fatty, being insoluble in ether, but they behave with re-agents in such a manner, as probably to be particles of this substance. Its atomic composition is identical with that of starch, dextrin, and grape sugar, $C_6H_{10}O_5$, but its general properties are intermediate between those of starch and dextrin. Like dextrin, when dissolved in water, glycogen is immediately transformed into grape sugar by albuminoid ferments, as is proved by the solution then decomposing the salts of copper, and turning the rays of polarised light to the right hand, and also by its readily passing into the alcoholic, or the lactic acid, fermentation.

An amyloid or cellulose substance was long ago found in the Tunicated animals (Schmidt), and amyloid bodies have since been observed in other Non-vertebrate animals (Carter). In a peculiar degeneration of various tissues and organs of the human body, as of the nervous substance, muscles, liver, spleen, kidneys, prostate, and other parts, amyloid bodies, or so-called *corpora amylacea*, have been frequently met with (Virchow, Mekele, Rouget). Bernard himself detected a glycogenic substance in the placenta, and in various embryonic tissues, especially in the muscles, though he thought it disappeared from them in after life. Amyloid substance is sometimes certainly present in healthy muscle; it has been found in the muscles of the horse a few hours after feeding, though, in the fasting condition, none is present. The occur-

rence of a starchy substance, is, therefore, as Rouget believes, by no means confined to the tissues of vegetables, nor even to the liver amongst the animal organs, but this substance may, under certain conditions, be a product of the nutritive action of nearly all the tissues.

The glycogenic function of the liver is, however, most remarkable, and constitutes a special assimilative office, super-added to its ordinary use of secreting bile. Since neither glycogen nor sugar is found in the bile, it is obvious that, if this animal starch be employed in the economy, it, or some product of it, must enter the blood, either directly through the veins, or indirectly through the lymphatics. It is now known that, not the glycogen itself, but the sugar resulting from its transformation, is absorbed by the hepatic veins. The detection of considerable quantities of sugar in the blood of the hepatic veins and of the right auricle of the heart, led, indeed, to the discovery of the glycogenic function of the liver. At first it was supposed by Bernard, that the sugar itself was formed by that organ. That this is not derived directly from starch or sugar in the food, is shown by its occurrence in animals killed after being fed, for at least a month, on meat alone. That the sugar comes from the liver, is shown by the fact, that after injecting water into the portal vein, until the fluid escaping from the hepatic veins, is colourless and free from sugar, it is possible, after waiting a certain number of hours, to obtain, by injecting more water, a further supply of sugar. Hence Bernard concludes, not merely that the sugar is produced in the liver, but that it must be formed by a slow, chemical, and not necessarily vital, change of an amyloid substance within the liver. By treating the liver substance in the mode already mentioned, the glycogen is then obtained separately.

The transformation of starch into sugar, by salivin, suggested the idea that this glycogen of the liver, also requires a special ferment to induce its metamorphosis. It was thought that, if not the salivin or pancreatin, this ferment might be some albuminoid product of one of the ductless glands; but extirpation of the salivary glands or pancreas, of the spleen, supra-renal bodies, thyroid, or thymus, in a series of experiments on animals, threw no light on the question (Schiff). The albuminoid substance is probably formed in the liver itself; for, whereas glycogen, like starch or dextrin, is not easily transmissible through the coats of the hepatic vessels, it is probably con-

verted into the readily dialysable sugar, before it is taken up by those veins. The fibrin and albumen of the blood, whether arterial or portal, will also convert dissolved glycogen into sugar. A boiling temperature destroys the power of the ferment, whatever this may be.

It has been suggested by Pavy that, although an amyloid substance abounds in the liver during life, no sugar, or but very small traces of it, are then present in this organ; and that, except in disease, transformation of the hepatin into sugar is, for the most part, a post-mortem result. This observer found no great difference in the quantity of sugar in the various large bloodvessels, either in the arteries, or in the hepatic or portal veins; the quantity detected was very small, averaging about $\frac{1}{16}$ th of a grain in 100 grains of blood. In the liver substance itself, macerated, instantly after death, in caustic potash or in very cold water, no sugar could be detected, though the hepatin or glycogen was then extracted. Most physiologists, however, coincide with Bernard, in believing that the formation of sugar in the liver, is constantly taking place during life; and that the accompanying decomposition of the glycogen into sugar, may explain the relative higher temperature of the blood, which has been observed in the hepatic veins.

The average quantity of sugar obtainable from the liver of the horse and calf, varies from 4 to 2 per cent.; in the rabbit's liver, it is about 2·5 per cent., and in Man, as noticed in healthy, recently executed criminals, about 2 per cent (Bernard). By others, sugar has been found in the liver of Birds, Reptiles, and Fishes, though in the cold-blooded animals the quantity is small; it has even been detected in the liver of the Mollusca (Bernard). It is more easily obtained from the veins than from the substance of the organ. The relative proportion found in the portal blood, in the systemic venous blood, and in the arterial blood of animals fasting, or fed only on flesh, is about ·06 parts in 100; whereas, in the hepatic blood, the quantity is usually about 1 per cent. In fully fed animals, especially after a meal containing starch, the quantity in each kind of blood is increased. In one experiment on a well-fed horse, killed soon after digestion, the proportion of sugar found in the liver, was nearly 2·3 per cent.; whilst that in the hepatic vein, was about 1·1, in the lymph ·44, in the chyle ·22, and in the blood generally ·065 (Poiseuille and Lefort).

The glycogen of the liver, being admitted to be the source

of the sugar found in the hepatic blood, the origin of the glycogen itself is yet undecided. Some have questioned the power of animal tissues, to form an amyloid substance, and have suggested that the glycogen of the liver is derived from the starchy matter of the food, which might be supposed, in Herbivorous animals, to be partly accumulated, in a modified form, in the hepatic cells or elsewhere. More sugar certainly, is obtainable from the livers of Herbivorous, than from those of Carnivorous animals, and more from Herbivorous animals recently fed on amylaceous food; but glycogen continues to be formed in the livers of fasting or actually starved animals, and of animals fed for a month, or more, exclusively on flesh. In such instances, the glycogenic substance found in the liver, cannot be derived directly from food, but is formed by some action of the hepatic cells, in which, as already mentioned, minute grains, apparently of an amyloid nature, have been detected. The constituents of the flesh used as food, which can be thus metamorphosed by the hepatic cells, are fat and albuminoid substances; for the small quantities of amyloid matter sometimes found in flesh, and of inosite or muscle-sugar always present in it, which is incapable of the alcoholic fermentation and does not turn the rays of polarised light, are not sufficient to produce it. By some, it has been supposed that the hepatic cells have the power of decomposing the neutral fats of the food, into glycerin and the fatty acids, stearic and oleic; furthermore, that the former is the source of the glycogen, and that the latter assist in the formation of the fatty acids of the bile: thus, 2 of glycerin, *i. e.*, $2(C_3H_8O_3) + 2$ of oxygen (O_2), are equal to 1 of glycogen ($C_6H_{10}O_5$) + 3 of water $3(H_2O)$. It has been objected to this, that the formation of sugar and of bile in the snail, has been observed to be an alternately performed function (Bernard). Another mode of origin of the glycogen from fatty matter, supposes that the conjugated fatty acids of the bile, tauro-cholic, and glyco-cholic acids, are first formed, that they are then re-absorbed from the intestinal canal by the portal vein, and are decomposed into glycogen and a nitrogenous product, which is ultimately converted into urea, and eliminated by the kidneys; for dogs with biliary fistulæ, appear to have no glycogen in the liver, and other dogs, after long fasting, if fed with taurin, show an abundance of glycogen in that organ. By some, again, albuminoid principles are supposed to be decomposed in the hepatic cells; according to one view, the products are glycogen and

the two conjugated biliary acids, one of which contains nitrogen, and the other, in addition, sulphur; according to another view, they are glycogen, and various nitrogenous bodies, such as creatin, creatinin, and other substances, which are ultimately excreted as urea. The continuous formation of sugar in the eggs of birds, during incubation, shows that glycogen may be formed independently of amylaceous food, and its origin from albuminoid matter, is rendered probable from the fact, that in animals fed on fat or oleaginous food alone, or even on pure starch, as distinguished from vegetable food containing starch mixed with other constituents, the glycogen is much diminished in quantity (Stokvis); whereas, in those fed on gelatin, it is almost normal in quantity, and attains its maximum in animals fed on highly albuminous diet (Bernard and Schmidt). The experiments of Dr. Pavy alone give opposite results, showing the greatest amount of sugar in animals fed on vegetable food only; but the increase of sugar then observed by him, might be partly owing to sugar formed from the food itself. He found, in the livers of dogs, the proportion to be about 7 per cent. with a pure animal diet, 14.5 per cent. with meat and sugar, and 17 per cent. with a purely vegetable diet. It is believed that the glycogen found so abundantly in the muscles of the embryo, the inosite formed in the muscles after birth, and the small quantity of glycogen which they contain after the liver has commenced its glycogenic office, are also derived from the decomposition of albuminoid substance into glycogen, and some oxidisable nitrogenous body, such as creatin or creatinin.

The *use* of the glycogenic function of the liver, is supposed to be that of continuously supplying an easily oxidisable material for the purposes of maintaining animal heat and motion. Sugar is a very unstable element in the presence of oxygen with albuminoid substances, such as are found in the blood. As already stated, the quantity of sugar found in arterial blood, that is in the blood which has passed through the lungs, is much smaller than that in the hepatic venous blood. Besides undergoing oxidation, like the sugar of the food, so as to form carbonic acid and water, the liver-sugar may also be capable of transformation, through the assimilative force of some of the animal tissues or organs, into fatty matter, or some other substances necessary to the living economy.

The sugar may likewise act as a solvent of the carbonate and phosphate of lime in the blood. It has also been said to aid in

the decomposition of albuminoid, into oleaginous or other compounds.

When animals are covered with varnish, which arrests the cutaneous transpiration, and interferes with the respiratory changes and the development of animal heat, both the sugar of the hepatic blood, and the glycogen of the liver, soon disappear; but, by then employing artificial warmth, they may be again formed. In hybernating animals, in which the respiratory process is also reduced to a minimum, the formation of sugar continues, but its oxidation, after it passes into the circulation, is imperfectly carried on, or entirely ceases, so that it accumulates in the blood, and even appears in the urine. So too, in the disease known as diabetes mellitus, the sugar found in that excretion, is supposed to depend upon the accumulation of sugar, probably of liver sugar, in the blood; for, in such cases, other secretions and excretions also exhibit traces of that substance. That the sugar excreted by the kidneys in diabetes, is not formed in those organs, is certain; and it has been noticed, that if the blood contain $\frac{1}{3}$ of a grain of sugar in 100 grains, this substance is no longer completely consumed, or oxidised, in the combustive processes of the economy, but appears in the various secretions and excretions, most abundantly in that from the kidneys. In the diabetic condition, not only may the sugar formed in normal quantity, accumulate, from not undergoing decomposition, but the liver may generate more sugar than usual.

A temporary and remediable diabetes may occur from the undue ingestion of sugar, or sugar-forming substances, with the food. Moreover, many medicinal agents appear to determine an increased activity of the glycogenic function of the liver, producing an artificial diabetes; such are, morphia, strychnia, and phosphoric acid in large quantities (Pavy). Asparagus has a similar effect; so likewise has the injection of various stimulating fluids into the portal vein (Harley), and the inhalation of acetone and benzine. Caustic potash and carbonate of soda check the formation of sugar (Pavy).

An experiment, first made by Bernard, in which an artificial diabetes is produced, shows that certain parts of the nervous system influence the sugar-forming function (vol. i. pp. 356, 394). It illustrates the power of the nervous system over the nutritive and assimilative processes, and may explain certain cases of ordinary diabetes. By passing a needle through the back of the occipital bone in the rabbit, and irritating with

its point, the floor of the fourth ventricle, from near which the deep roots of the pneumogastric nerves spring, he produced an artificial diabetes mellitus. Moreover, irritation of the cerebro-spinal axis, from the cerebral peduncles down to the roots of the pneumogastric nerves on the sides of the medulla oblongata, increases the formation of sugar in the blood, and gives rise to temporary diabetes. On the contrary, division of the pneumogastric nerves in the neck, that is, above the point where their branches to the lungs are given off, appears to restrain the formation of sugar in the system; section of the spinal cord below the origin of the phrenic nerves, has apparently a similar effect.

It has been suggested that these effects are not direct upon the liver itself, but that, in the normal condition, a certain stimulus, perhaps associated with the demand created by the process of oxidation going on in the lungs, proceeds from those organs, through the pneumogastric nerves to the medulla oblongata, and is thence reflected through other nerves, to the liver, where it excites or regulates the glycogenic action. On interrupting the continuity of this nervous chain, by division of the pneumogastric nerves, the formation of sugar is checked. Disturbances in the respiratory function, induced through the nervous system or otherwise, may favour the formation of sugar and its accumulation in the blood, and so produce diabetes. It is said, furthermore, that division of the great splanchnic nerves, or of the sympathetic nerves in the neck, increases the formation of sugar in the liver; this may depend, not on an increased formation of glycogen, but on the increased quantity of blood then admitted to the liver, owing to dilatation, through the action of the vasomotor nerves, of the small arteries of the abdominal viscera generally. The larger flow of blood through the portal system and liver, may change the glycogen already formed, into sugar, more quickly than usual, and thus favour its more rapid escape from the hepatic cells. This explanation may also apply to the effect of irritation of the back of the medulla oblongata, in the floor of the fourth ventricle; for the vasomotor sympathetic nerve fibres of the viscera of the abdomen, have been proved to pass down, in that part of the medulla, from the cerebral peduncles and optic thalami (Schiff).

The formation of glycogen by the liver, its conversion into sugar, and the entrance of this into the blood by the veins, establish the importance of this gland in the process of Sangui-

fication. These facts also suggest the possible occurrence of some similar, but yet unknown, actions in other secreting glands, and also in such tissues as muscle and nerve, as well as in the ductless glands.

Sanguification and the Blood Glands in Animals.

In the Vertebrata generally, the processes concerned in the formation of the white and red corpuscles, and the fluid matrix of the blood, are similar to those which occur in Man. Besides an absorbent system, the blood-glands, or ductless glands, are found in all the Vertebrate Classes, but they do not all exist in every Class. The spleen is almost universally present; the supra-renal capsules disappear earlier in the descending scale, the thyroid body and the thymus still sooner.

The *spleen* is present in all cases, excepting in the myxine fishes. It always possesses its peculiar structure and characteristic dark red colour; it varies much in shape, even in Mammalia, being, in different cases, round, oval, much elongated, lobulated, or even multiple. The latter condition is seen in the dolphin. The existence of supernumerary spleens, or *splenculi*, in dogs, cats, and other animals, has been already mentioned. In Birds, the spleen is small, and either round, oval, fusiform, or flat; in Reptiles, Amphibia, and Fishes, it is of variable size, and differs in form according to the general shape of the body. In Birds and Reptiles, this organ is usually attached to the pancreas; in Reptiles and Fishes, it is rather connected with the intestine than with the stomach, as in Mammalia. The existence of the Malpighian bodies, is doubtful in the Amphibia, and denied in Fishes; but the large aggregated blood-cells exist in all Vertebrata.

The *supra-renal* bodies are present in all Mammalia, Birds, Reptiles, in most, if not all, Amphibia, and in all but the lowest Fishes. They are always of a yellowish, ochreous, or golden hue. In Mammalia, they are of various forms, commonly three-sided, but often elongated, cylindrical, oval, round, or even crescentic. They are sometimes a little removed in position from the kidneys, as in the elephant and seal. They are large in Rodentia, and small in Carnivora, especially in the seal; their size, as compared with the kidney, is, in the guinea-pig, as 1 to 4; but in the seal, only as 1 to 150. In the Cetacea, they are lobulated, and supernumerary supra-renal bodies are met with in many animals. In Birds, these organs are small, and often lobulated. In Reptiles, they are usually placed on the renal veins, or vena cava inferior; in the Ophidia, the right one is the larger. In Batrachia, they are very small, broken up, or often indistinct, and embedded in different parts of the kidney. In Fishes, too, when present, they are usually small and multiple, and often found even at the back of the kidney; in the sturgeon and the Cyclostomatous fishes, their existence is doubtful.

The *thyroid* body is attached to the larynx in the Mammalia only. In Birds and Reptiles, it is placed low down in the neck, or even in the chest, near the inferior larynx. Its position seems to be regulated rather by its vascular connections, than by any peculiar relation to the proper larynx. In Reptiles also, it is in the thoracic cavity, close above the heart. As to Fishes, it has been supposed that the vascular organs

known as *pseudo-branchiæ*, attached to the branchial apparatus, are the homologues of the thyroid body; but the balance of evidence is opposed to this view, and if the thyroid body exist at all, it is only occasionally, as a small isolated mass, lying on the *bulbus arteriosus*.

The *thymus gland* is well marked in the *Mammalia*, being either confined to the thorax, as in the *Carnivora*, *Insectivora*, and *Marsupialia*, or having also shorter or longer cervical cornua, or extensions upwards into the neck, as in *Quadrumana*, *Bats*, *Rodents*, *Solipeds*, and especially in the *Ruminants*. In the ox tribe, its cervical part extends up to the lower jaw, forming the *neck sweetbread*, and, from the calf, is the part sold as the best sweetbread. This organ is a conjoined bilateral mass; its structure is lobulated and sacculated, as in Man. It is largest in the young animal, and disappears later in life. It is said to become larger in hibernating animals. In *Birds* it is represented, but only in the chick and young bird, by a small tube, having slight dilatations upon it; but it is sometimes divided off into sacs. In young *Reptiles*, it has also been found, and likewise in the tadpoles of most *Amphibia*; but not, it is said, in the siren or proteus, in which the lungs are the least developed. In *Fishes*, the thymus is absent.

In the *Amphioxus*, none of those ductless glands are found, not even the spleen; in this animal, no coloured blood-corpuscles exist.

In the *Non-vertebrata*, these glands and coloured blood corpuscles are equally absent; nor is any organ recognised in them, as being specially concerned in the process of sanguification. The liver, however, is almost universally present, and its glycogenic function has been detected in the snail; and as it is a blood gland, forming blood corpuscles in the *Vertebrate* embryo, it may suffice for the wants of the *Non-vertebrate* organism, in reference to the formation of blood. Such organs as the spongy masses around the great veins in the *Cephalopods*, may, perhaps, be concerned in sanguification.

SECRETION.

SECRETION IN GENERAL.

Secretion (*secernere*, to separate) is the separation, by a gland or membrane, of certain materials, in a more or less fluid state, from the blood, and their escape, by means of proper ducts or openings, or from a smooth membrane, on to the surface, or into the interior, of the body. This general process is, however, divisible into *secretion proper* and *excretion*. In *secretion proper*, the products are formed by a nutritive process, the result of a special attractive, selective, or assimilative power, possessed by some epithelial structure; and moreover, after being discharged from the mouths or ducts of the glands, or from the surface of membranes, they are used for certain purposes in the living economy. In *excretion*, the *educts* are

rather *eliminated* from the blood through the agency of special structures, also epithelial; and they are henceforth cast out from the body as effete, useless, or even injurious substances.

Secretion may be performed by glands, or by membranes; but excretion is always effected through the agency of glands.

The secreting glands are the liver, pancreas, the salivary, and lachrymal glands, the true mucous glands of the nose, mouth, fauces, pharynx, œsophagus, and duodenum, the simple tubular glands of the stomach and intestines, other minute glands associated with the ducts of some of the larger glands, the sebaceous and meibomian glands, and lastly the mammary glands. The secreting membranes are the mucous, serous, and synovial membranes. The excreting or excretory glands are the kidneys, and the sweat glands of the skin; to a certain extent, the liver, and perhaps the intestinal tubuli, especially those of the great intestine; perhaps, also, the sebaceous cutaneous glands; and, lastly, the lungs, which may be viewed as excreting glandular organs, destined to eliminate carbonic acid from the blood.

In certain forms of *secretion*, the separated products closely resemble those contained in the blood itself, such as the albumen of the serous and synovial fluids. Thus, the serous and synovial secretions consist of little more than the transuded materials of the plasma of the blood, unaltered in chemical character, but modified in their relative proportions. The casein of milk, is also merely a modified form of albumen. In other more special secreting processes, there are formed, not as mere transudations, but as the result of peculiar assimilative actions, substances not present in the blood itself, but, nevertheless, little removed in chemical character from its albuminoid constituents; such, *e.g.*, as the pepsin, pancreatin, and salivin of the gastric juice, pancreatic fluid and saliva, and the mucin of the mucous glands. The three former substances are, by some, regarded as examples of an albuminoid compound undergoing retrograde chemical changes, or in peculiar states of hydration. In other cases, the substances formed by secreting glands, though more remote in chemical constitution from that of the materials of the blood, and not pre-existent in it, are of a highly complex nature, and are only partially reduced or oxidised substances, such as the tauro- and glyco-cholic acids of the bile, the butyrim of the milk, and the fat of the sebaceous secretion. Extreme examples of special secretive power, by which compounds not existing in the blood, are

formed from it, are afforded by the appearance of sulphocyanogen in the saliva, and of hydrochloric acid in the gastric juice. So, also, soda is withdrawn from the normal soda salts of the blood, by the agency of the liver, to combine with the fatty acids of the bile.

In the case of the *excretions*, however, the characteristic substances eliminated from the blood, pre-exist in that fluid, as the result of decomposition, and are always much more chemically reduced by oxidation, than any product of secretion, or they are even completely oxidised. They usually exhibit a comparatively simple atomic constitution, are often crystallisable, and frequently take the form of bases or acids, such as the lactic and uric acids, and the urea, formed in the urine, together with the sulphates and phosphates resulting from the oxidation of the albuminoid constituents of the body; such also as the lactate of ammonia, and the acetic and formic acids of the cutaneous excretion; and lastly, the perfectly oxidised carbonic acid, given off in small quantities by the skin, but forming the characteristic product excreted by the lungs. Such substances are manifestly incapable of animal organisation. They are even, if retained in the system, noxious, or fatal. The purpose of excretion, is, indeed, to rid the body of the compounds which are formed during the action of the living tissues, by the oxidation of their substance, or of the blood passing through them. The successive stages of oxidation, render such compounds more and more removed from an organisable character, and necessitate their removal.

In all the secretions, if one excepts the peculiar albuminoid substances, the saline substances and other special compounds, are either crystallisable, such as the sulphocyanide of potassium in the saliva, the soda salts of the biliary acids, and the lactin or sugar of the milk, or crystalloid, such as the hydrochloric acid, and other acids in the gastric juice. All these would freely dialyse from the blood, or from the secreting cells. As to the modified albuminoid substances, which are colloidal, such as salivin, pepsin, pancreatin, and casein, it is possible that the secreting cells may themselves burst, and yield up their albuminoid contents; or the secretion of such substances from the blood, may present us with examples of the metastasis of colloidal substances from the pectous to the liquid, or from the liquid to the pectous state, as occasion may require.

In the process of excretion, it is, as already mentioned, the highly diffusible crystalloids alone, which escape from the

blood, so that it may more readily be referred to a pure dialysis, the one condition necessary, say, in the secretion of urea, *e.g.*, being a special chemical relation between the dialysing epithelial cells and the dialysable urea, which serves to locate the excretion of that substance in the kidney.

In the formation of living vegetable tissues, crystalloids, such as ammonia, carbonic acid, and water, are converted into colloids, and the further processes of organisation, up to the final and highest nutritive stage, require various metastases of these colloids. In the downward step of disintegration and disorganisation, materials are formed, which are to be excreted, and then the crystalloid condition of matter again prevails, as in the urea and uric acid thrown off by the kidneys, which easily pass into ammonia, and the carbonic acid and water of the cutaneous and pulmonary exhalations.

The general forms of the secreting and excreting glands, and the mode in which those forms may be derived from the involution of a simple secreting membrane, have already been described (vol. i. p. 70). In all cases, there is invariably found, even in the ultimate ramifications of the gland ducts, a limiting or basement membrane covered by a stratum of epithelial cells. All glands are, moreover, very vascular, and receive large quantities of blood. The special secretions and excretions are the products or educts of special organs. The most essential modifications of the anatomical gland-elements, are those which relate to the epithelial cells. In secretion proper, these important elements are frequently dissolved or ruptured, and their contents, if not their envelopes, escape as part, perhaps an essential part, of the secretion itself, as in the case of the saliva, pancreatic fluid, gastric juice, and milk, and of the sebaceous and the mucous secretions, and also, perhaps, of the bile. But in the case of the lachrymal secretion, and in the excretory processes generally, this is not so; for the epithelial cells in the ducts of the kidney, the lachrymal gland, and the sweat glands, and also, it may be added, in the air-cells of the lungs, merely withdraw, as it were, by a special attraction, certain products already pre-existing in the blood, and part with them again, into the ducts or canals, which convey them out from the body, without themselves undergoing any necessary dissolution or decay.

The liver receives a peculiar venous blood, loaded with the products of the venous absorption of the food, and with those which enter the blood of the spleen; but, with this exception,

the cause of the differences between the several secretions, cannot depend on the character of the blood distributed to the respective glands, which is uniformly pure arterial blood. Neither can it depend upon the number or arrangement of the capillary vessels, for these peculiarities can only determine the quantity, not the quality, of a given secretion. Nor is there any evidence to show that the walls of the capillaries differ in different glands, nor even the basement or limiting membrane, which always presents a glass-like, structureless, appearance. Again, the relative simplicity, or complexity, of a gland cannot be supposed, in any way, to determine the character of its secretion; for, though differently formed glands, supplied by the same blood, often yield different secretions, yet there are cases, in which very similarly formed glands produce different secretions, as, for example, the salivary, pancreatic, and mammary glands. Moreover, on regarding the Animal Kingdom generally, it is found that similar secretions, as, *e.g.*, the bile, the gastric secretion, and indeed nearly all the secretions, are formed, in different cases, by glands of variable structure, sometimes complex, sometimes simple, according to the position of the animal in the scale of organisation. There is one component, however, of all secreting and excreting organs, whether membranous or glandular, viz., the epithelial layer, which appears to be essential to specific secretion, and to be the seat of the selective *assimilative* power of the true secreting glands, and of the selective *eliminative* power in the excretory glands. The epithelial cells of different membranes and glands, most frequently present differences of structure and arrangement, suggestive of the possession of different properties. The peptic and hepatic cells, the columnar cells of the intestinal tubuli, and the cells of the sebaceous cutaneous glands, are totally different from each other. Even in the simplest glands in animals, as in the so-called hepatic tubuli, special epithelial cells are discernible. Epithelial cells are components of the solid texture of the body, subject to the ordinary processes of development, growth, and nutrition; but they are distinguished by a peculiar destiny or purpose in the economy, and to them we must refer that special form of nutrition, which, instead of resulting in the development or maintenance of a tissue, destined for certain mechanical or vital purposes in the animal framework, is employed for the formation, or separation, of more or less liquid products, intended for digestive or other uses, or

destined to be eliminated, and entirely discharged, from the system.

Most frequently, the gland-cells effect changes in the materials which are presented to them by the blood; but, at other times, they attract from that fluid, compounds which pre-exist in it. In either case, it is these cells which attract or separate the *products* or *educts*, from the circulating fluid.

The *general conditions* which influence the functions of secretion and excretion, are the quantity of blood supplied to the respective glands, the quality of that blood, the presence of external stimuli, acting directly or indirectly on the nerves, and perhaps some governing influence of the nervous system itself.

As a rule, an increased *quantity of blood* supplied to a gland, determines an increase in the amount of its secretion, as is illustrated by the increased redness of the gastric mucous membrane observed, in the case of the Canadian voyageur, Alexis St. Martin, during the active secretion of the gastric juice, and by the increased vascular turgescence of the mammary gland during lactation. As in ordinary nutrition, however, the secretive demand, implied by an increased secretive act, precedes the actual flow of additional blood to a given gland.

The influence of *quality in the blood*, is perhaps greater in regard to the excreting than to the secreting glands, as might indeed be expected. The presence of a greater or less quantity of the special materials to be separated and eliminated from the blood, must have a direct effect. An excess of urea or uric acid in the blood, whatever may be its cause, determines an increased elimination of those products from the kidneys, and an increased consumption of water, augments the quantity of the renal excretion. A temporary increase of carbonic acid in the blood, owing to the rapid oxidation of combustible substances, is followed by an increased evolution of that gas from the lungs; whilst the drinking of water augments the pulmonary exhalation and the cutaneous transpiration. The various secretions are also modified in quantity, by the amount of fluid absorbed from the stomach; and the relative amount of their characteristic ingredients, is dependent on the existence of certain proportions of particular blood constituents from which they are derived, as seen in the production of the fatty acids of the bile, and of the sugar, and the peculiar fatty acids of the milk.

The effects of *stimuli*, are chiefly to be noticed as influencing the quantity of a given secretion, as in the case of a flow of tears, induced by a foreign body irritating the conjunctiva, or of saliva, from the action of vinegar, mustard, or salt. Stimuli act probably through the intermediation of the vasomotor nerves, either directly, or else by reflex action, through other nerves and nervous centres with which the vasomotor nerves are connected. The general effect of such stimuli, is to dilate the small arteries of the gland; a corresponding increase then occurs in the flow of blood to it, and is the proximate cause of an increased secretion or excretion. This increase may, as in the case of the saliva, augment the quantity but not improve the quality of the secretion, which becomes more watery than usual.

There are many facts which show an intimate relation between the *nervous system*, and the secreting activity of the several glands. Thus, the emotions often determine increased secretion, as *e.g.* from the lachrymal glands, the skin, the alimentary mucous membrane, and the kidneys. The sight, or even the idea of food, will excite the flow of saliva. Extreme passion or grief has been known to modify, or even render poisonous, the mammary secretion. Direct experiments also show most remarkable effects produced upon the secretive process, through the nervous system, as illustrated in regard to the salivary glands (vol. i. p. 333; vol. ii. p. 56), the gastric glands (vol. ii. p. 61), and the liver (vol. ii. p. 340).

All glands are provided with sympathetic nerves, and many, if not all, possess others derived from the cerebro-spinal nervous system. The experiments just referred to, show that the *quantity* of a secretion is differently affected by the section, or irritation, of these two sets of nerves. Thus, irritation of the pneumogastric nerves, increases the quantity of the gastric juice, whilst irritation of the sympathetic nerves, diminishes or arrests it. Again, division of the sympathetic nerves of the submaxillary gland, increases the flow of saliva, but irritation of the distal cut portion of the nerve, diminishes it; on the other hand, section of the cerebral nerve, diminishes, whilst irritation of the distal cut end, augments it. Even simple irritation of the undivided sympathetic nerves, causes diminution, whilst a similar irritation of the undivided cerebral nerve, causes an increase of the secretion. Since, in the former case, the small arteries of the gland contract, and the supply of blood is diminished, whilst in the latter, those

vessels dilate, and more blood is distributed to the gland, the diminution or augmentation of the secretion, accords, in either case, with differences in the quantity of blood conveyed to the gland, and the influence of the nervous system in regulating the quantity of the secretion, is indirectly manifested by the dilatation or contraction of the coats of the small arteries.

With regard to the influence of the nerves on the quality of a secretion, it is found that when the arteries are contracted, and the supply of arterial blood lessened, not only is the quantity of saliva diminished, but the colour of the venous blood returning from the gland, is, as usual, dark; whereas, when the arteries are dilated, the supply of blood is increased, and the amount of secretion augmented, then the colour of the returning venous blood, is bright. In the former case, the passage of the blood through the gland, seems to be sufficiently deliberate, to permit of the proper nutritive or secretive interchanges between it and the epithelial cells; whilst in the latter case, the blood flows so rapidly through the glands as not to undergo these changes. It is not proved that the sympathetic nerve determines, or even increases, the secreting power of the gland.

By controlling the quantity and velocity of blood passing through a gland, the sympathetic nerves may, therefore, not directly, but indirectly, by permitting the characteristic function of the gland, preserve the essential *qualities* of its secretion; whilst, on the other hand, the cerebro-spinal nerves, by determining an increased supply and quicker motion of the blood, must, by partially interfering with, or overwhelming, the special actions of the secreting cells, increase the fluid in the secretion, but so dilute and lower its qualities.

Whilst it is not yet proved that either the sympathetic, or the cerebro-spinal, nervous system has any power over the chemical acts of secretion, independently of their governing influence over the bloodvessels, it must be added that this is a point on which opinions are at variance. As already remarked (p. 284), if, as it seems scarcely possible to doubt, the nervous system influences the secreting processes in such of the lower animals as are unprovided with bloodvessels, and yet possess nerves, it is difficult to deny the existence of some such direct influence in the higher vascular animals and in Man, however unintelligible the nature of such a controlling process may be.

Whatever the influence of the nervous system upon secre-

tion, it may be centric, or peripheral, and either simple or reflex, according to the part in which the stimulus originates, or to which it is applied. Tears are shed, and saliva flows, under the centric stimulation of painful or joyous emotions, and on the occurrence of ideas relating to food; whilst the same secretive acts are performed under reflex action, from neuralgia of the fifth cerebral nerve, or from local irritation of the conjunctiva or of the mouth.

When, either from disease of the glands, or from an over-accumulation, in the blood, of the materials to be excreted, these are no longer eliminated through the usual organs, they are sometimes vicariously eliminated through some other gland or membrane. Thus, urea has been found in almost every secretion and excretion of the body, in the gastric and intestinal discharges, in the lachrymal and salivary fluids, in the nasal mucus, in the synovial and serous fluids, the perspiration and even in the milk. The pigment of the bile, which is probably more of an excretory than a secretory product, occasionally appears in the renal excretion and in other fluids of the body. These are instances of real vicarious excretion, but in regard to the secretions proper, no such metastasis, or transference, of secreting power has been observed, no authentic example of milk secreted by the liver or kidneys, or of saliva formed by the mammary gland, having yet been met with. The presence of the colouring matter of the bile in various true secretions, as in the pancreatic juice, the milk, the mucus of the bronchial glands and membrane, and even in the serous and synovial fluids, is perhaps only an apparent example of vicarious secretion; for, in these cases, the colouring matter of the bile is probably re-absorbed into the blood, and then is simply exuded into all parts of the body with the common nutrient plasma, and so tinges the various solid tissues, organs, glands, and secretions. There is, moreover, no evidence that, even in these cases, the more abundant and truly secretory products of the hepatic cell action, viz. the soda salts of the biliary acids, accompany the bile pigment in its passage through the body, or into the secretions of other glands. The biliary pigment probably represents an excretory part of the bile, and, if not preformed in the blood, is easily dissolved and taken up by it, and thus it may obey a true metastasis like other excretory substances. It certainly appears very readily in the urine, and also sometimes in the perspiration.

Certain excretions are complementary to each other, as, for example, those of the lungs and the liver. The more abundant the excretion of carbon in its perfectly oxidised form of carbonic acid gas from the lungs, the smaller is the amount of carbonaceous compounds excreted in the bile; whilst, on the other hand, when the respiratory changes are diminished through heat of climate, or defective exercise, the biliary products are increased. The excretions of the skin and the kidneys, are also, to a certain extent, complementary to each other, not only as regards their aqueous constituents, in respect of which, each is, moreover, supplemented by the lungs, which give off more or less vapour according to the relative degree of moisture of the air, but also in regard to some of the products of oxidation of the albuminoid tissues, viz., urea, ammonia, and carbonic acid.

Different secretions and excretions differ as to the time at which they are prepared. Some are constantly or continuously formed, whilst others are secreted, or excreted, intermittently, or remittently. Secretions are more commonly intermittent or remittent, serving occasional purposes in the economy, as, *e.g.*, the gastric juice, the secretion of which is probably limited to the period of digestion, and the lachrymal, salivary, hepatic, pancreatic, and mammary secretions, which are always being secreted in small quantities, but are, from time to time, as required, produced in much larger amounts. On the other hand, the excretions being injurious, and requiring to be eliminated, as rapidly as possible, from the blood, are characterised by their constant separation both day and night, the process varying in activity, however, according to circumstances.

The *force* by which the secretions are urged along the ducts, is probably the *vis à tergo*, dependent upon the pressure of continuously fresh-formed portions of fluid secreted in the commencing ducts. The movement in the larger ducts, is aided by the slow contraction of the organic muscular fibres in the walls of the ducts. In some cases, as in the bile and pancreatic ducts, and the ureters, rhythmic movements have been seen, and in others, peristaltic movements. The pressure on the fluid in the ducts, is sometimes considerable, as is seen by the occasional ejaculation of the saliva, and the expulsion of the milk. The action of the surrounding muscles, must, here and elsewhere, also be taken into account. In certain cases, the larger ducts are dilated near their mouths, into temporary receptacles for the secretion, as is seen in the parotid and

lactiferous ducts. Still more special developments of the excretory apparatus, are met with in the shape of reservoirs or bladders, with contractile walls, when, as in the case of the bile, the secretion is abundant and used intermittently, or when, for other reasons, an excretion requires to be retained, and only occasionally expelled.

The daily quantities of the various secretions and excretions, as stated elsewhere in the account of each, differ remarkably in different individuals, and in the same individual under different circumstances. The quantities of the excretions, in health, conform to the quantity of water taken in the solid and fluid food, one of the objects of this elimination of water, being to maintain the due characters of the blood. In the formation of the extraordinary quantities of the secretions employed in the digestive process, the water concerned is, as already mentioned, separated from the blood, used in dissolving the food, re-absorbed, and re-secreted many times over.

The preceding facts and considerations, illustrate the general resemblances and differences between nutrition and secretion. In both processes, the blood yields a common plasma to certain organs; from this plasma, in both, materials are attracted by a selective property possessed by pre-existing tissue elements; and, in both, the residual and altered plasma re-enters the blood. But this difference arises: in the one, the separated materials form an intrinsic part of a solid and more or less permanent tissue, and enter into the coherent framework of the body; whereas, in the other, whilst a part thus remains to form the gland-tissue itself, the essential products are discharged, in the fluid state, by ducts, and are applied extrinsically, to special functions of the economy, sometimes, however, being then re-absorbed into the blood. Both the nutritive and the secretive process yield various results, according to the tissue in which they occur; nutrition forms nerve, muscle, or bone, and secretion, saliva, pancreatic juice, or milk, according to the nature of the tissue elements which select, or determine, the separation of the nutrient or secreted materials, from the blood plasma. Both nutrition and secretion are modified by the quantity and quality of the blood, and by the reactions of the vasomotor nerves. The nutritive and secretive processes may both be either continuous or intermittent, the former being illustrated by the continuous formation of the epidermis and of mucus, and the latter by the intermittent nutrition of the muscular and nervous tissues and the forma-

tion of the gastric juice. Lastly, the two processes resemble each other, in being more active in some parts than in others, being more so, in the heart, the nervous centres, and the salivary glands and sweat glands, than in the tendons, cartilages, bones, and the mucous and sebaceous glands.

SPECIAL SECRETIONS.

Most of the secreting glands and their products, have already been considered, viz. the lachrymal glands and the tears, with the appendages of the eyes; the nasal glands, with the organ of smell; the ceruminous glands, with the ear; the sebaceous glands, with the skin; and, lastly, the mucous glands of the mouth, fauces, pharynx, œsophagus, stomach, and duodenum, the saliva and salivary glands, the gastric and intestinal tubuli and their secretions, the liver and pancreas and their respective products—with the organs and function of Digestion. The tracheal and bronchial mucous glands will be mentioned hereafter, in the Section on Respiration. There remain, however, certain general considerations concerning the liver and its offices, which may be here noticed; whilst the mammary glands with the function of *lactation*, and the mucous, serous, and synovial secretions also require description.

Secreting Function of the Liver.

The source of the bile secreted by the hepatic cells, is the exuded plasma of the portal blood, which, however, is joined by the blood from the nutrient capillaries of the liver, derived from the hepatic arteries. That the portal blood is essential, and the arterial blood non-essential as such, to the formation of bile, is proved by the facts, that when the portal vein is compressed, the quantity of bile is diminished, and that when it is tied, bile is no longer secreted; whereas, if the hepatic arteries be tied, its secretion is not necessarily arrested (Schiff). In certain cases of malformation, the portal vein has been found to open into the inferior vena cava, and yet bile has been secreted. Hence the portal blood has been held to be non-essential to the formation of bile; but, in such cases, the umbilical vein is permeable, and sends branches through the liver; moreover, the blood of the hepatic arteries, having first become venous, may enter the lobular plexuses, and so secrete the bile.

That the biliary acids are not preformed in the blood, but are elaborated in the hepatic cells, is shown by extirpating the liver in frogs; these animals then survive for some days, and yet no trace of the fatty acids of the bile is found in the blood, which would be the case, if the bile were preformed in, and merely separated as an educt from, that fluid. The green colouring matter, and also cholesterin, may, however, pre-exist in the blood. The cholic acid may be derived from the fats of the blood, whilst the taurin and glycocoll, which are conjugated with it, the former containing both sulphur and nitrogen, and the latter only nitrogen, probably arise from the decomposition of albuminoid substances. The colouring principles may be formed from the cruorin, or colouring matter of the blood, which they closely resemble. Animals fed on fat, have been said to secrete proportionally more bile; but this is denied, and the quantity of albuminoid food consumed, seems rather to regulate the amount of this secretion.

Besides its office in digesting fat, and stimulating the muscular acts concerned in digestion and absorption, the bile has other uses. The fatty acids, largely reabsorbed, may become converted, in the circulation, into carbonic acid and water, for respiratory, motor, and calorific purposes. The glycocoll, taurin, and the colouring matters are apparently excreted. The glycocoll is probably thrown off by the kidneys as urea, for when it is administered as food, more urea is then eliminated; the colouring matters, altered from a yellow to a greenish, and then to a dark-brown hue, some taurin, and likewise a small portion of the cholic acid, converted into dyslysin, are found amongst the excreta. The excrementitious character of the bile, is further indicated by the size and activity of the liver before birth, when no digestion is going on. Moreover, by its glycogenic function, the liver performs a highly important nutritive office, affording to the body respiratory food. Lastly, it may be said to act as a purifying agent on the venous blood returning from the alimentary canal, partly by its direct power of assimilating albuminoid, oleaginous, saccharine, and colouring substances, but also partly as a sort of filtering organ, in which foreign bodies, such as metallic salts and other substances, are detained, and prevented from entering too suddenly into the general circulation.

Irritation, or division, of the pneumogastric nerves, below the diaphragm, appears to produce no effect on the quantity of the bile secreted in a given time; but injury to both, or even

to one of those nerves higher up, interferes with the biliary secretion, perhaps by its effect on the circulation and respiration.

When the bile is not eliminated from the system, or when it is reabsorbed, symptoms of nervous prostration ensue, with headache and jaundice, often followed by death. The constituents of the blood, out of which the bile is formed, when retained, or the bile itself when taken up, appear, therefore, to be noxious, or even poisonous.

The combined assimilative, secreting, excreting, and purifying actions of the liver, are consistent with its large size, its general presence in nearly all animals, its marked vascularity, the peculiar source of its blood, the high temperature of its tissue and of the hepatic blood returning from it, and the singular variety of the metamorphic changes which take place in it. So long as its office was supposed to be merely to secrete 2 oz. of solid *biliary matter* daily, whilst the lungs excrete 8 oz. of *carbon* in the same time, the size and other characters of this gland, were not fully explained, especially in its embryo state; but its glycogenic function, and its influence in the process of sanguification, sufficiently account for its pre-eminence amongst all the glandular organs of the body.

The Mammary Glands and Lactation.

The human infant, and the young of all *Mammalia*, are supplied with suitable nutriment for the first months of their existence, in the well-known fluid named *milk*, secreted by the *mammary glands*. It is in the female only, that these glands yield milk, the process being termed *lactation*. In the males of mammiferous animals, these glands exist, but their parts are very small.

The mammary gland, in woman, is a large organ, composed of numerous lobes, arranged, in a more or less radiating manner, around the projecting part, named the *mammilla*, or *nipple*. The lobes, which may be moved slightly upon each other, are separated by fibrous septa, and are held together by a general investment, stronger on the under side of the gland, where it rests upon the pectoral muscle. Each lobe consists of a number of lobules, possessing the structure of a compound racemose gland, closely resembling that of the parotid gland (fig. 42, c). The terminal ducts end in clusters of short follicles, or vesicles, about $\frac{1}{200}$ th of an inch in diameter,

which, when filled, are just visible to the naked eye, and the walls of which are lined with a layer of soft glandular epithelial cells. From these follicles, the smallest lactiferous ducts unite into one or more larger ducts for each lobule, and these join into still larger tubes called *galactopherous* ducts, one or more for each lobe. These large ducts, about fifteen in number, run to the centre of the gland, and generally dilate, so as to form temporary receptacles for the milk. The walls of these ducts are composed of a fibrous coat, containing unstriped muscular fibres, and lined by a mucous membrane continuous with the skin. They open at the summit of the nipple, by separate small round orifices, seen at the bottom of little depressions in the skin. The arteries of the mammary gland are numerous, and proceed from many sources; they present a good example of the enlargement of bloodvessels supplying a part, in which increased activity of function occurs. Numerous capillaries surround the terminal vesicles of the gland. The veins and lymphatics are also numerous. So likewise are the nerves, partly spinal, and partly sympathetic, the latter reaching the gland along the arteries.

The first secretion of milk is preceded by an enlargement of these glands, which causes a certain hardness and tenderness of the part, and a febrile disturbance of the system, known as *milk fever*. The first milk secreted, much thicker and darker than the subsequent secretion, is named the *colostrum*. After lactation is established, the secretion is not uniform, but remittent, proceeding slowly during the intervals of suckling, so as not usually to accumulate and cause suffering, but suddenly increasing, in accordance with the great afflux of blood to the glands, during the act of nursing. The fulness and increased secretion experienced at this time, constitute the phenomenon called the *draught*. From each distended gland, the quantity obtainable by pressure, is about two ounces; but the daily quantity secreted by both, fluctuates according to so many circumstances, that no correct average is attainable. The composition of the milk, also varies exceedingly. Its specific gravity ranges from 1,030, or less, to 1,035. The colour of human milk, is bluish-white, owing to its greater transparency as compared with cow's milk. It is opalescent, and perhaps fluorescent. It contains from 860 to 910 parts of water in 1,000, the solid matter varying accordingly, from 14 to 9 per cent.; its average composition is 89 parts of water to 11 of solid constituents. These latter consist of 4.5 of lactin or

sugar of milk, 3·5 of casein, 2·5 of fatty matters or butter, ·3 of extractives, and ·2 of alkaline and earthy salts, together with traces of iron. Milk likewise contains, like the blood, carbonic acid gas, nitrogen, and oxygen, the total amount of these gases being about 3 per cent. of its volume; more than half of this is carbonic acid gas, and only $\frac{1}{2}$ th part oxygen, the remainder being nitrogen.

The milk is a true secretion, formed out of the materials of the exuded plasma of the blood, by the agency of the epithelial cells of the terminal vesicles of the gland. It is composed of a slightly turbid fluid, containing suspended in it, a vast number of minute, more or less spherical, particles named the *milk globules*; these are composed of an oily matter, surrounded by a thin film or pellicle of albuminoid substance, probably of casein, for neither ether nor an alkali, which would dissolve fatty matter, attacks them, unless they are first acted on by acetic acid, or are strongly agitated, so as to dissolve or break the albuminoid film, which does not appear to be organised. These milk globules vary from $\frac{1}{12000}$ th to $\frac{1}{3000}$ th of an inch in diameter; other and much smaller spherical particles, manifesting the molecular movement, exist in the fluid, and probably cause its turbidity; some of these may consist of casein, but they are chiefly fatty, and readily dissolve in ether. The milk also contains a few epithelial cells from the ducts. Owing to the thin pellicle around the milk globules, these do not at once run together, but only coalesce, after a time, in the formation of the cream. In the colostrum the milk globules are very minute, but there also exist in it, peculiar large, yellowish, closely and finely granular fatty corpuscles, which resemble the so-called exudation cells, or compound inflammation cells; these appear to result from the fatty degeneration or transformation of the glandular epithelial cells. The colostrum contains albumen, or at least it coagulates on boiling; it also has a larger proportion of sugar and saline constituents. It exercises an aperient effect upon the new-born infant. The colostric condition sometimes persists for too long a period, and then the milk is less suitable for food.

As long ago remarked by Prout, milk presents us with a type, or pattern of food, for it contains, in definite and duly balanced proportions, nitrogenous and non-nitrogenous nutrient substances, albuminoid, fatty and saccharine, fitted for both plastic and respiratory purposes, and, besides these, suitable salts for the blood and tissues. Milk, as we have

seen, is composed of water, which holds in *solution* lactin or milk-sugar, casein or the albuminoid substance characteristic of this secretion, certain extractive matters, and salts; whilst it contains, in suspension, fatty with albuminoid matter. When set aside in quantity, a natural analysis of milk takes place; first the oily matter, being of light specific gravity, together with a certain amount of casein, and even sugar and saline substances, rises as *cream*, the globules of which, by agitation, as in the process of churning, combine to form *butter*, leaving most of the casein, the sugar, and other substances, extractives, and salts, in the *butter-milk*. After a time, some of the sugar in this butter-milk, undergoes a peculiar fermentation, perhaps excited by the casein, and is changed into *lactic acid*; this immediately precipitates the casein in minute flocculi, which combine to form the so-called *curd*. The residual fluid, called the *whey*, now contains most of the lactin or sugar of milk, with lactic acid, extractives, and salts.

The fatty matter of the cream, consists chiefly of olein, but it also contains stearin, and, in particular, a peculiar fat, named butyrin, which is a compound of butyric acid and glycerin, and imparts to butter its characteristic taste and smell. It yields, when acted on by alkalies, and also when spontaneously decomposed at high temperatures, besides butyric, small quantities of caproic and capric acids. The casein of human milk, is not so easily precipitated by acids or by rennet, as the casein of cow's milk; in this respect, and also as regards its smaller quantity of casein, human milk resembles more closely the milk of the ass. The lactin or sugar of milk, which may be separated by crystallisation from inspissated whey, is convertible into grape-sugar, by dilute mineral, or by vegetable, acids; it is very prone to enter into the lactic fermentation, and even to form butyric acid by decomposition; but it is difficult to transform it into alcohol. The extractives of milk have not been well examined. The salts resemble those of the blood; but they present curiously a larger relative amount of the earthy phosphates of lime and magnesia, which are combined with, and rendered soluble by, the casein. Chlorides of sodium and potassium, and traces of phosphate of iron, are met with. Human milk may be either neutral, alkaline, or acid; but the milk of most animals usually, and that of the Carnivora always, at the time of its examination, is acid, from the presence of free lactic acid.

The casein is probably formed, by the secreting power of

the mammary gland cells, from the albuminoid principles of the blood ; but, according to some, it is preformed in the blood itself, during the period of lactation. It supplies materials to the infant, for the re-formation of albuminoid compounds. The oily matters derived from the animal fats, or from sugar, and the sugar itself, the source of which is yet unknown, are not only directly adapted for respiratory purposes, and the production of animal motion and heat, in the infant, but also, as well as the casein, are doubtless employed, in part, in various important nutritive and secretive processes. The salts of the milk are also those which are essential to the formation of blood, salts of potassium and iron for the corpuscles, and salts of soda, calcium, and magnesium for the liquor sanguinis. The phosphates of lime and magnesia are absolutely necessary for the growth of the young skeleton. Of all the secretions, milk is especially nutritive, and most closely resembles blood in composition, its chief distinction from that fluid, being the large quantity of sugar in it. Milk alone contains albuminoid, fatty, and saccharine elements combined. Its secretion is not essential to the system, being, ordinarily, limited to one sex, and, in that, being temporary or periodic. From its general resemblance to blood, the arrest of its secretion, is not so pernicious as the non-secretion of the bile ; nevertheless, its retention within the gland, besides causing obstruction of the ducts, inflammation of the organ, and its consequences, may likewise, perhaps, prove injurious through re-absorption, especially of the crystalloids, lactin, and lactic acid. It has been supposed that its constituents may be retained in the blood, and so account for the constitutional disturbance which follows the sudden arrest of the secretion ; but the proper constituents of the milk are probably not, normally, pre-existent in the blood, though they may, like those of other secretions, be reabsorbed. Cases of vicarious secretion of milk, which are very numerous, may depend on reabsorption, and distant exudation, of the absorbed constituents. A case has been recorded of the expectoration of milk following sudden arrest of the secretion. Instances of so-called vicarious secretion of milk from the inguinal region, have been supposed to be due to the presence of supernumerary mammary glands in that position. This would correspond with the normal situation of these glands in some of the lower animals, and rudiments of more than one pair of mammary glands, are sometimes met with in the human body.

The quantity and quality of the human milk, vary according to many circumstances. Thus, it is not only most abundant, but most nutritious, in nursing women, from the age of 15 to 20, whilst it is least so, in those from 35 to 40. The constitution also greatly influences the character and nutritive qualities of the milk; hence the necessity for the selection of healthy wet-nurses. In the early periods of lactation, the casein is at first relatively small in quantity, but afterwards becomes increased and attains a determinate ratio; whilst the sugar is at first abundant, but afterwards reduced in proportion. From experiments on the cow, the fatty matters seem to vary most, chiefly according to the nature and quantity of the food, the temperature in which the animal lives, and the amount of exercise it is permitted to take. Thus, warmth and rest, increase the quantity of oily matter, whilst cold and exercise diminish it (Playfair). Exercise, however, increases the relative amount of casein. Both in the human subject and in animals, the nature of the food, and the quantity of water taken in, or with, it, must directly influence the specific gravity, the amount of solid matter, and the relative quantities of the several ingredients of the milk. It has been observed in the cow, that the last milk drawn, at any one time of milking, is richer than the first.

The influence of the nervous system in modifying the quantity and quality of the milk, is most important, and universally recognised. Irritation of the nipple increases, by a reflex influence, the flow of milk; this is probably one cause of the rapid flow of the secretion during the act of suckling. Continued local irritation, combined with a strong desire for the occurrence of lactation, and a fixed attention towards the mammary glands, have been known to produce this secretion in women not recently mothers, to protract its flow for many years, to excite it in aged women and in girls, and even, it is said, in individuals of the male sex. In that sex, usually, however, the rudimentary glands yield only occasionally a thin clear fluid, the composition of which is uncertain. The influence of the nervous system, as affected by mental states, upon the secretion of the milk, is further evinced by the abundant flow, the so-called draught, often excited by the sight, or even by thinking of the infant. Tranquil and pleasing emotions favour the normal secretion; but anger, anxiety, grief, and terror may produce serious modifications in the quality of the milk, or may even suspend

its formation. Violent passion may induce such changes in this secretion, as to cause it to be poisonous, and even immediately fatal, to the infant. This probably arises from some modification in the blood (p. 318).

To secure the healthy performance of the function of lactation, an ample amount of nutritious food, moderate exercise, tranquillity of mind, and regular habits, are necessary conditions; a defective or excessive diet, fatigue, and irregularities and excesses of all kinds, are unfavourable. The influence of alcoholic stimulants, in moderation, is, by promoting digestion indirectly, favourable to the supply of milk. Medicinal agents, especially those of a powerful kind, should be avoided; many of them enter the milk, and may thus affect the child. Mineral and saline substances, and the alkaloids, such as quinine and morphia, pass more readily into the milk than vegetable aperients.

The peculiarities in the milk of the cow and other animals, as compared with human milk, are interesting in a dietetic and economic point of view:—

	Woman (Simon)	Cow (Simon)	Goat (Chevalier)	Sheep (Chevalier)	Ass (Simon)	Mare (Luiscius)
Water	890	860	868	856	907	888
Solid matters .	110	140	132	144	95	112
Butter	25	38	33	42	12	8
Casein	35	68	40	45	16	16
Sugar, with ex- tractives }	48	30	53	50 }	65	88
Salts	2	6	6	7 }		

According to this Table, the milk of the *goat*, more closely resembles, in chemical composition, the human milk than does that of any other animal; but it has been found that, besides having a peculiar odour, its curd is remarkably compact. The milk of the *sheep*, differs a little more from human milk. That of the mare and of the ass, are characterised by the small quantity of butter and casein, and the large quantity of sugar, which they contain. The milk of the mare, is most remarkable for its enormous proportion of sugar; this may explain its disposition to undergo the alcoholic fermentation, a fact turned to account by many Tartar tribes, in order to make an intoxicating drink. The milk of the ass, notwithstanding its difference from human milk, is, perhaps from the difficulty with which its casein is precipitated, and from the delicacy of its curd, the most easily digested by the human infant. Cow's milk, which is the great source of milk for human food and the great substitute for human milk in the case of infants, contains more casein and more butter than human milk, but only about 3-5ths of the quantity of sugar. The specific gravity of good milk is about 1030, that of the cream being 1024, and that of the skimmed milk about 1035; by means of a proper lactometer, the quality of milk may be determined

approximately by every householder. Considered as infant food, the milk of the cow, is too rich in casein and butter, and too poor in sugar; hence it should be diluted and sweetened, either with common white sugar or, what is better, with sugar of milk. Half a pint (imperial) of good fresh cow's milk, with half an ounce of milk-sugar and half a pint of water, will form a tolerably near approximation to ordinary human milk, but it is deficient in the due proportion of saline, earthy, and ferruginous salts. As an infant advances in age, the sugar and water may be diminished, and farinaceous food may be added. It is well known that the milk of certain breeds of cattle, is richer than that of others. Authorities differ as to the relative richness of the milk of cows fed in town dairies or in country pastures, but country milk must be more natural, and better as food, than the artificially forced production of the town-fed animal, other circumstances being equal.

The mammary glands, as is well known, differ in arrangement and position in different orders of Mammalia; sometimes, as in the Carnivora and in the pig, they are divided into numerous portions, disposed along nearly the whole length of the under side of the trunk, each symmetrical mass having its own nipple; sometimes, as in the Ruminants, and in the genus *Equus*, they are post-abdominal; in the Cetacea, they are situated even still further back; in the Quadrumana, as in Man, they are found in the pectoral or thoracic region only. The microscopic structure resembles that of the human gland, excepting in the lowly organised Monotrematous *Ornithorhynchus*, in which the milk glands consist merely of clusters of simple blind follicles, opening in a group on the skin. This simple structure suggests an homologous relation between the mammary and the cutaneous glands.

Mucous Secretion and Mucus.

Mucus is the clear, or slightly turbid, colourless, viscid fluid found on mucous membranes. It is partly secreted by the epithelial cells of the compound racemose glands, but in part, also, by those of the surface of such membranes. It is a special secretion from the plasma of the blood, and differs from it chemically. Mucus is commonly alkaline, but often speedily becomes acid; normally, perhaps, it is neutral. It is composed chiefly of water, holding in it from 4 to 6 per cent. of solids. It contains desquamated epithelial cells, mucous corpuscles which closely resemble the white blood corpuscles, and pus corpuscles, and also certain nucleated cells intermediate between the true mucous cells and epithelial cells. Its chief constituent is a special albuminoid substance, called *mucin*, which, precipitable by alcohol, acetic, and other acids, but not by boiling, swells up, rather than dissolves, in water, and is the cause of its natural viscosity; besides this, it contains a small amount of extractives, and salts like those of the blood. It is sometimes very thin, as when secreted from

the nose during a cold; in other situations, it is much more viscid, as the intestinal or vesical mucus, and the nasal mucus; that from the air passages in cases of cold, is very viscid, and contains albumen. The use of mucus, is chiefly mechanical, assisting in the acts of mastication, deglutition, or speech, or, as in certain animals, in the capture of prey. It aids in taste and smell, preserving the moisture of the parts, and acting also as a solvent. It is likewise protective, both mechanically and chemically, by offering resistance to the action of the digestive fluids, which do not easily dissolve it. Sometimes it behaves as a ferment, possibly assisting the salivin, pepsin, and pancreatin, though not possessing very active powers. It, or something mixed with it, undoubtedly determines the retrograde decomposition of the renal excretion, when this is retained longer than usual in the body. Mucin, not being readily soluble or digestible, cannot, strictly speaking, be nutritive or absorbable.

Serous and Synovial Secretions.

These fluids, which cover and moisten the surface of the serous and synovial membranes, differ so little in composition, from the plasma of the blood, that their formation has, by some, been regarded, not as a process of secretion but as one of transudation through those membranes. A certain modification of the plasma of the blood, as it is exuded from the capillaries, is here accomplished, however, by the action of the epithelial cells, which, in a single layer, cover these membranes. These fluids may sometimes contain, in certain morbid conditions, excretory materials, such as urea, lactate of soda, sugar, and traces of bile pigment, all of which are manifest transudations.

The *serous* fluids, which must not be confounded with the serum of the blood, contain as much as 99 per cent. of water, a few salts, some albumen, and a substance slightly soluble in alcohol. They are thin and scanty in normal conditions, in the cavities of pleura, pericardium, peritonæum, and arachnoid spaces, their use being merely to prevent friction. The aqueous humour of the eyeball, may be regarded as a serous secretion, adapted, by its locality, to a very special purpose. When accumulated in abnormal quantity, from inflammation, serous fluids cause internal dropsies, and, in that case, generally contain traces of fibrin, which will slowly coagulate after removal from the body.

The *synovial fluid*, or *synovia*, is much more viscid than the serous fluid; it contains nearly 6·5 per cent. of albumen, together with fatty matter, salts resembling those of the blood, epithelial cells, corpuscles like the pale corpuscles of the blood, and, it is said by some, a substance closely resembling mucin. The use of this fluid, found alike in joints, in the so-called bursæ mucosæ, and in the sheaths of tendons, whether these move in grooves on the bones lined with cartilage, or in soft parts only, is chiefly mechanical, to prevent the effects of friction; but in the joints, it may act nutritively on the cartilages.

EXCRETION.

The characters which distinguish excretion from secretion proper, have already been detailed (pp. 343-5). Its products, like those of secretion, are fluid or gaseous, at least in the human body, although semi-solid, or solid, urine occurs in Birds and Reptiles. The term *excreta*, is also commonly applied to the solid materials ejected from the intestinal canal, as the residuum of the digestive process. These, however, are only partly excreted substances, such as unabsorbed biliary and other products more or less changed, substances thrown out by the intestinal glands, and undigested mucus and epithelium. The greater portion of the mass, however, consists of undigested food, such as elastic tissue, sarcolemma, the walls of vegetable cells, spiral ducts, and woody fibre.

The fluid excretions are those eliminated by the kidneys and the skin, the former excretion being the more complex. The exhalation of carbonic acid from the lungs, is an excretory process more immediately necessary to life than any other. The lungs may be regarded as excretory glands, and the carbonic acid expelled from them, as a gaseous excretion; but the speciality of this process, its association with the absorption of oxygen, and its peculiar mechanism, render it necessary to consider the entire function separately, under the head of Respiration.

Renal Excretion.

The urine, excreted by the kidneys, is the most perfect example of a fluid excretion given off by the animal economy; its

various constituents exist preformed in the blood; they are, moreover, highly oxidised nitrogenous products of the decomposition of the albuminoid tissues, and of the albuminoid constituents of the blood. They are destitute of organisation, and incapable of it; neither can they be made, in animals, to undergo an ascensive chemical metamorphosis fitting them for nutrient purposes; they are of no further use in the organism, and, indeed, if retained, are highly injurious to it. Hence they are destined to be, once for all, separated, or *excreted* from it, and to be, as soon as possible, entirely discharged from the body. It facilitates this end, that they are chiefly crystalloid bodies, and therefore easily dialysable. It is provided, moreover, that a very large proportion of the blood should pass through the organs by which these substances are eliminated, for the quantity sent through them in twenty-four hours amounts to nearly 2000 lbs. (Brown-Séguard); so that all the blood in the body, may pass through them 150 times in that period. Lastly, the excretion of urine is continuous or incessant.

The Kidneys.

The *kidneys* are two dense, firm, dark-red, solid, but fragile glandular organs, situated at the back part of the abdominal cavity, in the lumbar region, one at each side of the vertebral column, on a level with the last dorsal and the two or three upper lumbar vertebræ, and reaching from the eleventh rib to near the crest of the hip bone. The right kidney, owing to the proximity of the liver on that side, is about a rib's breadth lower than the left. The kidneys are placed behind the peritonæum, and are held in position by their bloodvessels, nerves, and the excretory ducts, called the *ureters*; they are likewise surrounded by an areolar tissue, usually loaded with fat, forming the so-called adipose coat, which, being a bad conductor of heat, serves to preserve the temperature of these organs. The shape of the kidney, is well known and characteristic. Each is about 4 inches long, 2 wide, and 1 thick; the left one is rather longer and thinner than the right. In the male, each weighs from $4\frac{1}{2}$ to $5\frac{1}{2}$ ounces; in the female, about $\frac{1}{2}$ oz. less. The left kidney is generally about $\frac{1}{4}$ oz. heavier than the right. The weight of the two glands together, in proportion to that of the body, is about as 1 to 240. The specific gravity of the kidney substance is 1050. Its chemical composition is 76 per cent. of water, 15 of albuminoid sub-

stance, only 1 of fatty or resinous matter, which is chiefly cholesterin, together with certain extractives, including inosite, cystin, taurin, and xanthin.

If one kidney be atrophied or destroyed by disease, the other one usually enlarges. In certain cases, the kidneys are joined by a transverse portion of gland substance, the upper border of which is generally concave, the resulting mass forming the so-called *horse-shoe kidney*. The two conjoined kidneys are sometimes found on one or other side of the lumbar region, or even in the pelvic cavity. A few instances are on record, of the presence of three kidneys, the third gland, usually called a *movable* or *floating kidney*, being placed either on one side of the vertebral column, or in front of it, or else in the pelvis.

The upper end of each kidney is surmounted by the corresponding supra-renal body. Its internal concave border presents towards its middle, a deep longitudinal fissure, called the *hilus*, which leads into a cavity within the organ, named

Fig. 109.

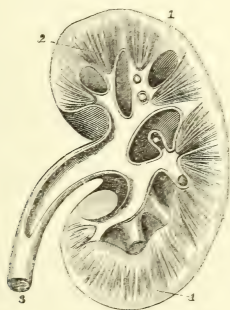


Fig. 109. Diagram of a longitudinal section of the kidney. 1. Cortical substance. 2. A pyramid. 2'. Mammilla or papilla of a pyramid, lying in its opened calyx. 3. Portion of ureter expanding above into the pelvis of the kidney, then dividing into the infundibula, and afterwards into the calyces.

the *sinus*. This gives exit and entrance to the bloodvessels, absorbents, and nerves, and also to the ureter; the renal or emulgent veins here lie in front, the ureter behind, and the renal arteries between them.

The kidney is everywhere closely invested by a proper firm, smooth, *fibrous coat*, which may be readily torn off; it is, however, connected with the gland substance, by numerous fine fibrous processes and vessels; it passes in at the hilus, lines the cavity of the sinus, and is even reflected on to the ureter and bloodvessels.

On making a longitudinal section of the kidney through the hilus, the solid gland substance is found to consist of an outer *cortical* portion, and of a deep-seated *medullary* portion. The *cortical* substance is continuous over the whole organ, and dips in between the different parts of the medullary portion, which is disposed in a series of conical masses. The cortical substance is about 2 lines in thickness, and forms about $\frac{3}{4}$ of the entire gland. It is of a reddish colour, soft, granular, and friable, and contains a number of little round dark-red spots, which indicate the position of certain minute bodies, named the *Malpighian corpuscles of the kidney*. The conical masses of the medullary substance, from fifteen to twenty in number, form the so-called *pyramids* (Malpighi). Their bases, turned towards the surface of the kidneys, and also their sides, are encompassed by the cortical substance; but their apices are turned towards the sinus, in the interior of the organ, where they form little eminences, called the *papillæ* or *mammillæ*. The substance of the pyramids, is firmer and darker than the cortical substance, and, as seen on a section, is striated from apex to base, the latter part being much darker than the former.

Outside the hilus, the ureter presents a funnel-shaped dilatation, or membranous cavity, called the *pelvis of the kidney*, which, as it passes into the sinus, divides into three tubes, named the *infundibula*; these again subdivide into from seven to thirteen smaller, also funnel-shaped, tubes, called the *calyces*, which surround, or embrace, the papillæ. One calyx often includes two, or even three, papillæ, so that they are usually fewer in number than the latter.

The cortical and medullary substances are both composed of minute closely packed *tubules* or *ducts*, the *tubuli uriniferi*, with bloodvessels, absorbents, and nerves, held together by a soft material of ill-defined structure. The latter is described as consisting of a very fine, scarcely recognisable, areolar tissue or stroma, more evident in the medullary portion, but forming, at the surface of the kidney, a thin layer beneath the fibrous coat; a parenchyma is also described by some. The different

appearance of the cortical and medullary substances, depends on the different arrangement of their ducts and blood-vessels.

In the cortical portion, the tubuli uriniferi are very numerous, much convoluted, and inosculate freely with each other; they are, on an average, about $\frac{1}{800}$ th of an inch in diameter, and are known as the *tubes of Ferrein*. They generally commence by free closed extremities; sometimes, however, they anastomose together, forming loops; many are said to begin as minute purse-like dilatations, which form little partial *capsules* around the Malpighian corpuscles (Bowman); nearly all are somewhere connected with these capsules. In the pyramids or medullary substance, the tubuli quickly unite together many times, dichotomously or by twos, and, becoming larger and straight, constitute the so-called *ducts of Bellini*; these form tapering bundles, directed to the papillæ, or apices, of the pyramids, on which they open by minute round orifices. It has been estimated that there are as many as two millions of tubuli in each kidney; that the number of orifices in a square line of a papilla, are 100; and that there are from 300 to 500 on the surface of a single papilla (Krause). The straight tubuli are widest near their orifices, measuring from $\frac{1}{250}$ th to $\frac{1}{400}$ th of an inch; they cause the striated appearance of the pyramids. The uriniferous tubules are composed of a transparent basement membrane, lined with a thick polygonal, or spheroidal, glandular epithelium, which occupies about two-thirds of the diameter of the membranous tube. The epithelial cells have very delicate walls, a roundish nucleus, fine granular albuminoid contents, and occasional fat, pigment, and other particles. This epithelial layer is continuous with that covering the free surface of the papillæ. In the coldblooded Vertebrata, it is, in parts, provided with cilia.

The *Malpighian corpuscles* of the cortical substance, are placed either at the free closed extremities of the convoluted tubuli, or in the course of the loops which these occasionally form. These little bodies, the *glomeruli* of Ruysch (1660), are spheroidal, and measure about $\frac{1}{120}$ th of an inch in diameter. Each is composed of a rounded, close coil of minute vessels, which projects, like a little ball, into one of the capsules of the tubuli. It appears that a minute branch of the renal artery, named an *afferent* vessel, reaches each Malpighian body, and, dividing into superficial coiled branches, forms a globular network; from the centre of this, an *efferent* vessel arises, and,

leaving the corpuscle, forms, with the efferent vessels from neighbouring corpuscles, a dense vascular plexus, which surrounds the contiguous tubuli. According as the capsule of the Malpighian corpuscle, is formed at the commencement, or on the side, of a tubule, it is said to be *lateral* or *terminal*. At the mouth of the capsule, the spheroidal epithelium of the tubule loses its character; for within the capsule, the epithelium is squamous and remarkably thin. It is said by some, to be continued over the surface of the Malpighian corpuscle which projects into the capsule (Gerlach, Isaacs). But according to Bowman, the corpuscle lies naked in the capsule, without any such covering, the afferent and efferent vessels being supposed to perforate the capsule. These vessels enter and pass out at nearly the same part of the corpuscle, which is there attached to its capsule. According to some observers, the efferent vessel is always *narrower* than the afferent one, and hence has arisen the idea that the blood is checked, or held back, in the coiled vessels of the corpuscle. The central vessels of the corpuscle, are, by some physiologists, regarded as capillaries, and the efferent vessel as a vein, which then breaks up to form the fine plexus around the adjoining tubule—an arrangement supposed to represent, on a very minute scale, a renal *portal* system. But all the coiled vessels, and even the efferent vessel of the Malpighian corpuscles, are, by others, considered to be arterial, the whole forming a microscopic *rete mirabile*, which ultimately, by the efferent vessel, ends in a true capillary network around the tubules.

The *renal* or *emulgent arteries*, right and left, spring from the sides of the aorta; they are short, and very large for the size of the kidneys, being out of proportion to the mere nutritive necessities of these organs. They soon divide into four or five branches, which pass between the pyramids, and are partly distributed, in the form of nutrient vessels, to the cortical and medullary substances, and to the common coat of the kidney; but they chiefly terminate in the Malpighian corpuscles, or in the fine vascular network which surrounds the tubuli. The *veins* accompany the arteries, and end, for each kidney, in a single large renal or emulgent vein, which joins the ascending vena cava. The *lymphatics* are numerous, and consist of a superficial and deep set. The renal *nerves* are small but numerous, and may be traced even on to the afferent arteries of the Malpighian corpuscles; but their mode of termination is unknown. They are derived from the sym-

pathetic nerves found on the renal artery, and from the lesser splanchnic nerve.

The ureter, its pelvis and calyces, are composed of an external fibro-elastic coat, continuous with the proper capsule of the kidney; of a muscular layer, which consists of external longitudinal and internal circular fibres; and of a mucous coat, continued on to the papillæ, and lined with a spheroidal epithelium. The ureters, in animals, contract slowly on the application of galvanism or other stimuli; sometimes they act rhythmically. Their lower ends enter, at each side, the fundus or base of the urinary bladder, penetrating its coats obliquely, and opening into it, by a narrow elongated orifice, so guarded by muscular bundles, that the reflux of urine into them is prevented.

Action of the Kidneys.

The purpose of the enormous number of uriniferous tubes, is, as in glands generally, to increase the extent of secreting or excreting surface, within a given space. It has been calculated that the total amount of surface in the coiled tubes in each kidney, exceeds forty-four square feet; and to this must be added, the excreting surface of the straight tubuli as well (Vierordt). The Malpighian bodies are quite peculiar to the kidneys, these little vascular coils, projecting into a duct, having no resemblance to the solid sacs which bear the same name in the ductless gland, the spleen. So special a structure has doubtless some special office. Since these bodies have been shown to project into the tubuli, at or near their commencement, it has been conjectured that they separate from the blood the greater part of the water of the urine, and that then, the inspissated blood which passes from them by the efferent vessel, enters the vascular plexus around the tubuli, and yields to the spheroidal epithelium, the proper solid constituents of the urine, which are thence excreted into the tubules themselves, and are washed away out of those canals, by the watery exudation descending from the Malpighian corpuscles. The naked condition of the glomerulus, and the squamous character of its epithelium, are fitted for a simple process of transudation; whilst the spheroidal epithelium of the tubuli is adapted to a true excreting office, though the walls of the tubuli must likewise excrete a little water. It is impossible to deny, moreover, that the glomeruli have also a true excreting office. It is now believed to be certain, that all the blood of the renal

arteries, goes through these Malpighian corpuscles, before it reaches the tubules, and if it then becomes inspissated, the blood which circulates around the tubules, may be compared to the portal blood of the liver, being, as it were, venous blood highly charged with materials destined to be separated from it. In support of the view that the Malpighian corpuscles separate the water, it has been urged that in Birds and Reptiles, in which the urine is partly, or almost entirely, solid—though in the Amphibia and Fishes, lower in the scale, it is again fluid—these bodies, though numerous, are remarkably small. Moreover, the analogy of the minute vascular arrangements within the kidney, with a portal system, is thought to be favoured by the fact that, in Reptiles, a branch from the hepatic portal vein is distributed to the kidney.

That some, at least, of the peculiar constituents of the urine, of which urea, uric acid, creatin, and creatinin are the chief, exist preformed in the blood, is certain; for the two latter are found in it, in considerable quantity, urea in smaller quantity, and uric acid perhaps only as an exceptional ingredient. It has been suggested that the urea and the other crystalloids present in the inspissated blood, may pass, by swift dialysis, into the aqueous contents of the tubuli; but though these substances, and urea especially, are highly dialysable, yet such a physical explanation of their separation from the blood, would not account for their special appearance in the renal excretion, rather than in any other, or, for the quantity eliminated from the system in a given time, considering how minute is the normal proportion of urea, and how much less that of uric acid, in the blood. It is, indeed, impossible to deny that the spheroidal epithelial cells of the tubes, have a special affinity for the proper urinary constituents; or, and this may be of more moment in explaining their appearance in the urine, that some of these substances are formed by the special metamorphoses of other materials within these cells. In the former case, the cells would merely select the urinary constituents from the blood, and transmit them into the tubuli; in the latter, they would, in addition, be the seat of special chemical decompositions. In the first case, for example, they might be supposed to separate pre-existing urea from the blood, but, in the latter, to metamorphose creatin or creatinin into urea. Indeed, after extirpation of the kidneys—an operation which animals will outlive a few days—the blood is not found to contain much urea, but to be rich in nitrogenous

extractive matters, which include creatin and creatinin. Moreover, if the ureters be tied, so that the escape of the urine from the excreting structure of the kidneys, is at first hindered, and at last prevented, urea is found in great abundance in the blood, as if its formation had gone on in the spheroidal epithelial cells, and it had been duly excreted, but then reabsorbed, or else had been absorbed from those cells directly into the blood.

It is further supposed that the smaller relative diameter of the efferent vessels of the glomeruli, and the unusual blood pressure in the renal arteries, may have an influence in the excretory work of the renal apparatus. By some, it is thought, that a selective or metamorphic power of the cells, is indicated by the fact, that uric acid salts are actually seen, in the cells lining the straight tubuli, in the kidneys of Birds. Whilst the products of the decomposition of the tissues, are passing from the inspissated blood of the vascular plexus upon the tubules, into the epithelial cells, some of the thin watery fluid within the tubes, is reabsorbed by those vessels, and thus the renal blood partly regains its fluidity, whilst the urine becomes more concentrated.

Under excessive pressure in the arterial blood-columns of the kidneys, as, *e.g.* when the aorta is tied below the points of origin of the renal arteries, albumen appears in the urine. The same event happens from obstruction of the renal ducts or vessels, or from the pressure of tumours upon them. This is not a dialytic process, albumen being a colloid substance, and difficult to dialyse; but it is probably an example of simple porous diffusion or filtration. In acute inflammatory conditions, fibrinous exudations from the blood, form in the tubuli, and appear in the urine, as minute coagula or *casts*.

The urine excreted into the tubuli, urged on by the vis a tergo of a constant process of excretion, escapes from their orifices into the calyces. From these, it descends along the infundibula, the pelves of the kidneys, and the ureters, into the bladder, partly by gravity, and probably partly propelled by the rhythmic peristaltic actions of the muscular coat of those canals. Accumulated in the bladder, it becomes further concentrated by absorption of water, and is mixed with mucus from the ducts and from that viscus.

The *constancy* and the great *rapidity* of the excretion of urine, have been observed in cases of malformation, known as inversion of the bladder, in which the lower part of the ab-

domen and the anterior portion of the urinary bladder are defective, so that the fundus of this organ, into which the ureters open, is exposed. Under ordinary circumstances, the urine is seen to flow in drops, from the mouths of the ureters; but, after drinking freely, it runs in little streams.

The urinary excretion is affected, both in quantity and quality, by the nervous system. Thus, it is increased in quantity, and lowered in quality, by hysteria, fear, and other mental emotions, this effect being probably due to dilatation of the renal arteries. Injury of the spinal cord, affects the urine, chiefly causing a great development of carbonate of ammonia and the precipitation of phosphates, owing, it appears, to congestion and inflammation of the bladder, with an increased secretion of mucus from it. Complete removal of the brain and spinal cord, in animals, does not much affect this excretion.

The walls of the bladder chiefly consist of layers of unstriped muscular fibres, collected into bundles, arranged like figures of 8, on the front, back, and sides of the organ. Some of these, surrounding the neck, act like a *sphincter*; the others form *detrusor*, or expellent muscles. The act of emptying the bladder, requires the simultaneous relaxation of the one, and the contraction of the other set. These are usually reflex acts, excited directly by the accumulated fluid, or by some irritation of the nervous system. The act of expulsion is aided by the contraction of the abdominal walls.

The Urine.

The daily quantity of fluid excreted by the kidneys of an adult healthy man, varies from 30 oz. to 80 oz.; but, on an average, it has been estimated at about 50 oz. This quantity varies according to the amount of fluid taken in the food and as beverage, the activity of exhalation by the skin and lungs, and the amount excreted by the intestinal canal. More fluid is excreted by the kidneys in winter than in summer, the skin being less active in the former, and more so in the latter, season. The quantity is said to be increased under higher barometric pressure. The specific gravity of the urine, differs much, not merely according to the different proportions, but also according to the different *nature* of its solid constituents; in health, it may range from 1015 to 1030; usually, however, it deviates only slightly from 1020. The urine excreted after

drinking much water, and taking little or no food, which is named *urina potûs*, is of course of low specific gravity; that after eating a full meal, is of high specific gravity, and is called *urina cibi vel chyli*; whilst after complete abstinence from both food and drink, as in the morning, it is most completely saturated with solid constituents, and is therefore at its highest specific gravity; it is then called *urina sanguinis*. The amount of solid constituents, is irrespective of that of the fluid, and depends on the activity of the metamorphosis of the tissues, and of the superabundant food. Its usual bright amber colour varies, according to its density, from that of a colourless fluid to a deep yellowish brown. In disease, the colour and specific gravity, present important variations; thus, in Bright's disease of the kidneys, the specific gravity may be as low as 1003, being little higher than that of water; its proper constituents are then deficient, whilst albumen, derived from the plasma of the blood, is present; on the other hand, in diabetes mellitus, in which the urine contains sugar, the specific gravity may be as high as 1050. The peculiar odour of the urine, is strongly developed by a heat sufficient to produce evaporation. The natural reaction of this fluid, is acid, but after digestion, and especially after a vegetable diet, it may become alkaline; in herbivorous animals, this is its normal character. The cause of its acidity, will be discussed after its chemical composition has been described. From a particular kind of decomposition, known as the acid fermentation, its acidity may be increased, after it has been excreted; on the other hand, by a decomposition of the urea, in which carbonate of ammonia is generated, it may acquire a strong alkaline reaction a few hours after its excretion, or even, in certain diseases, whilst it is yet retained in the bladder. In such a condition, an abnormal deposit of phosphates takes place.

Normal urine consists of water, holding a very variable quantity—viz. from 2 to 7 per cent.—of solid substances, of which urea is the chief; besides this, there are uric and hippuric acids, free carbonic acid, often lactic acid, occasionally oxalic acid, extractive nitrogenous matters, partly crystallisable, such as creatin and creatinin, xanthin, phenylic, carbolic, benzoic and other acids, uncrystallisable extractives of uncertain composition, small quantities of special pigments, traces of fatty matter, numerous salts, such as sulphates, phosphates and chlorides of potash, soda, lime, and magnesia, with silica, mucus, and epithelium. The relative proportions of its various

solid constituents in 100 parts, and the daily average quantity of each, excreted for every 1 lb. weight of the body, in a man weighing 145 lbs. avoirdupois, are shown in the annexed Tables.

Daily quantity for 1lb. weight of body substance, in a Man of 145lbs. weight (Parkes).

Water	2·9 drachms.
Urea	3·53 grains.
Uric acid	·059 "
Hippuric acid	·237 "
Creatin	·032 "
Creatinin	·048 "
Colouring matter, and other extractives	1·062 "
Sulphuric acid	·214 "
Phosphoric acid	·336 "
Chlorine	·875 "

Composition of 100 parts of the Solid Constituents (Lehmann).

Urea	49·68
Uric acid	1·61 grains.
Extractives: Creatin, Creatinin, Hippuric } acid, Salts of Ammonia, Chloride of Sodium }	28·95 "
Alkaline sulphates	11·58 "
Alkaline phosphates	5·96 "
Phosphates of lime and magnesia	1·97 "

The *water* of the daily urine, equals about one-half of that taken into the stomach; supposing the total quantity of the excretion to be from 30 to 50 oz., the water would be from 28 oz. to 47 oz. The *solid constituents* amount to from 2 oz. to 3 oz. in the twenty-four hours.

The *urea* is by far the most important and characteristic substance, amounting to upwards of an ounce, or half the solid constituents, in 24 hours, or, according to some estimates, to as much as 500 grains. Its atomic composition, $\text{CH}_4\text{N}_2\text{O}$, corresponds with that of carbamide, COH_4N_2 , and also with that of 1 atom of hydric cyanate of ammonia, viz. $\text{CNOH} + \text{NH}_3$. It is readily transmutable, by the absorption of the elements of two atoms of water, into carbonate of ammonia, one atom of which contains $\text{CO}_3 + 2(\text{NH}_4)$. Urea is thus obtained: evaporate cautiously a considerable quantity of urine to the consistence of syrup; to this, add slowly its bulk of nitric acid, when certain crystals are thrown down, which are nitrate of urea; dry these upon a filter, decolorise them by dissolving them in water, and boiling with animal charcoal, and recrystallise; once more dissolve the crystals, and now sepa-

rate the nitric acid, by means of carbonate of baryta. On evaporating the solution, a pasty substance is left, from which alcohol dissolves out the urea, and the filtered solution yields, on evaporation, pure crystals of this substance. These crystals are long, colourless, four-sided prisms, extremely soluble in hot, and even in cold, water; hence urea never enters into the composition of urinary sediments or calculi. It dialyses most actively. It is neutral in its reaction to test paper; but it acts as a base, combining with acids to form definite salts. As hydric cyanate of ammonia is identical in composition, crystalline form, and chemical properties, with urea, and as the former substance can be made in the laboratory, it affords an example of the imitation of an organic compound, by artificial means (Wöhler). Urea contains 46·7 per cent. of nitrogen, together with 20 per cent. of carbon. One ounce, taken as the ordinary daily excretion, contains about 220 grains of nitrogen.

The *sources* of the urea, are evidently nitrogenous organic compounds, which have undergone decomposition by partial oxidation. It constitutes the highest product of oxidation of the albuminoid and gelatinoid substances in the body. It is derived, partly from the tissues, but partly from the food, merely assimilated into blood; not, as was at one time supposed, from the tissues only. This is proved by many facts. Thus, the urea is always increased after meals, especially about three or four hours after the food is taken. In animals fed on too little nitrogenous food to counterbalance the waste of the albuminoid tissues, more urea is given off than the nitrogen in the food would form; when the waste is just compensated for, then the urea is equal to the nitrogen in the food; lastly, when an excess of nitrogenous food is given, the weight of the animal increases, and, after a time, an excess of urea is eliminated. Urea is still excreted, even in starving animals, though in smaller quantity than usual; it is increased by feeding them on a vegetable diet containing nitrogen, especially on bread and beans; its quantity is still greater, on a mixed vegetable and animal diet, but it is greatest of all, on an exclusively animal diet. In a dog weighing 30 kilogrammes, the daily excretion of urea, with a pure animal diet, varied from 150 to 180 grammes—that is, it equalled $\frac{1}{200}$ th or $\frac{1}{160}$ th of the weight of the body. In Man, with an exclusively animal diet, the daily quantity excreted was found by Lehmann to be about 820 grains, with a mixed diet 500 grains, with a vege-

table diet 347 grains, and with a completely non-nitrogenous diet 237 grains. The researches of Dr. E. Smith, confirm these results, and further show that an animal diet increases the excretion of carbonic acid from the lungs. In other experiments, the quantity excreted daily, on a superabundant animal diet, was found to be nearly 3 oz.; on a moderately animal diet continued for ten days, from $1\frac{3}{4}$ to 2 oz.; and after a diet of sugar, prolonged for four days, the daily quantity of urea was rather less than $\frac{1}{2}$ oz. Not only, then, is urea formed largely from the food, but chiefly so, the quantity derived from the tissues, as above shown, when a non-nitrogenous saccharine diet was taken, being less than half the ordinary daily amount. Sometimes even more is eliminated during a total abstinence from food, as if, in the latter condition, an animal maintained its temperature by waste of its nitrogenous tissues.

In the female, from her smaller frame, her less active nutrient metamorphoses, and the smaller quantity of food consumed, the daily quantity excreted is about $\frac{3}{4}$ of an oz. Proportionally to the weight of the body, it is less abundantly formed in women; but children up to seven years old, excrete about twice as much urea, proportionally, as adults, and infants more than children; in old age, the relative amount is diminished. The effect of age, depends upon the diminished activity of the nutritive functions, and the smaller quantity of the food. Exercise was formerly believed to increase the quantity of urea, and rest to have the opposite effect; but recent observations show that the immediate effect of exercise is to diminish the excretion of urea, though towards the end of labour, and especially in the period of rest afterwards, it is greatly increased. Gelatin, which seems never to be directly assimilated by the tissues, but rather to save them from oxidation, is readily, perhaps directly, converted into urea. Water, especially if taken with food, causes an increase in the ureal excretion, and also in that of the saline constituents of the urine. Diminished temperature and increased barometric pressure, are said to increase the quantity of urea. In most cases, the urea is not eliminated until some hours after its actual formation in the system, or until the determining cause of its increase, has taken effect. The quantity excreted is greater during the day than in the night. Common salt, phosphoric acid, theobromine, urea itself, uric acid, and cantharides, are found to increase the amount of urea excreted, whilst

tea, but especially coffee, alcohol, turpentine, and digitalis, diminish it. It is remarkable that such large quantities of nitrogen and carbon, are eliminated from the system in the form of urea—a comparatively inactive chemical substance; whereas carbonate of ammonia, a compound readily produced from the elements of urea, and an extremely irritating and noxious substance, is not formed in quantity, in the animal economy. In certain diseases of the kidneys, the urea is not excreted, but, the blood becoming vitiated, uræmic poisoning occurs, characterised by symptoms, such as convulsions and coma, referrible to the nervous centres, and often fatal. It was formerly supposed that the urea itself is the toxic agent, but possibly it is the carbonate of ammonia derived from the decomposition of the urea. In these cases, ammonia is found in the breath, and, after death, in the blood; the injection of that substance into the veins of an animal, also causes similar symptoms. A dilute solution of urea, to which a small quantity of mucus or other animal substance is added, readily ferments, and, evolving a pungent odour, forms carbonate of ammonia; this kind of fermentation may take place very rapidly, even within the bladder. The amount of urea increases in all those diseases which are accompanied by an increase of tissue change, such as active inflammation of the lungs, or of the membranes of the brain, and in fevers generally, even though less food and exercise are taken than in health. In fever, the quantity has been found to be double the ordinary amount, viz. 1065 grains daily; in pyæmia, it has reached 1235 grains (Vogel and Warnecke). During recovery, the quantity excreted falls for a time, although more food and exercise are taken.

Uric acid is found not only in the urine, but also in the blood, and in most organs of the body. It contains 33·3 per cent. of nitrogen, and has the following composition: $C_5H_4N_4O_3$; it is therefore regarded as resulting from a less complete oxidation of the nitrogenous compounds of the food and of the body, than that which produces urea. The formation of urea in the system, is supposed, by some, to be normally preceded by that of uric acid. The former may be easily produced from the latter, by processes in which oxidation forms a part; when an alkaline urate is digested with portions of liver, at a certain temperature, urea is formed at the expense of the uric acid. Animals to which uric acid is administered with the food, excrete an unusually large quantity of urea. Some of the

products of the metamorphosis of the muscular tissue, such as creatin, xanthin, and sarcin, have affinities with uric acid. Lastly, in a state of rest, the quantity of uric acid excreted, increases, whilst the urea ultimately diminishes, the reverse being the case from exercise.

The quantity of uric acid excreted daily, has been estimated at from $8\frac{1}{2}$ to 15 grains; but this, like the quantity of urea, varies very much, most markedly according to the amount of nitrogenous food which is taken, and less so according to the age and sex. Its quantity is lessened by exercise. With animal diet, its quantity is said to be 4.5 grains, and with vegetable diet, only about 1.5 grain daily (Haughton.) In the urine, it is either combined with soda, forming the urate of soda which is held in solution, or else it is dissolved by the alkaline phosphate of soda. Being less soluble than its salts, uric acid is quickly precipitated by acids, and moreover, being itself less soluble in cold than in warm water, it is commonly precipitated from normal urine after cooling. This may be partly from the diminished solvent power of the cooler fluid, and partly from the occurrence of the lactic acid fermentation. Uric acid is then precipitated and deposited, either in an amorphous powder, or in fine crystals of peculiar forms, often tinged with colouring matter. The crystals are sometimes little flattened rhomboids, sometimes they resemble a coffin or a barrel, and sometimes they are almost spherical. It forms the most common urinary sediment, and the most frequent kind of renal or vesical calculus or stone in the kidney or bladder. Hence it is also named *lithic acid* (*λίθος*, a stone). Urate of soda constitutes the solid urinary excretion of Serpents, and is also present, in large quantity, in the white pasty portions of the dejecta of the flesh and fish-eating Birds, such as the hawks and owls, the penguins and other sea-birds. Hence it exists in large quantity in guano. It may be obtained pure from human calculi, or from the solid excretion of the serpent, by dissolving the urate in those substances, in a hot solution of caustic potash, and reprecipitating it from the filtered fluid, by means of another acid. The precipitate is a white powder, composed of colourless rhomboidal scales; it is almost insoluble in cold water, and only slightly so in hot, and is absolutely insoluble in alcohol and ether; it is soluble in alkaline solutions, and very readily in solutions of lithia. From all these solutions, it is immediately reprecipitated, even by feeble acids. Heated nearly to dryness with

nitric acid, uric acid turns red, and, on the addition of ammonia, a beautiful purple substance, named *murexid*, is formed, a reaction which constitutes a test for uric acid. The fact that uric acid is a less perfectly oxidised compound than urea, explains, perhaps, its formation in excess under certain conditions, as, *e.g.* when the quantity of tissue metamorphosed, or the quantity of food taken, is greater than the supply of oxygen can convert into urea, as, *e.g.* in acute inflammations, rheumatism, and gout, in all which diseases, large quantities of uric acid deposits, or of urates, are thrown down from the urine, which is loaded at critical periods, after the climax of the attack. At the onset of the gout, the uric acid sometimes nearly, or entirely, disappears from the urine; it may then be detected in the blood. The gouty concretions, known as chalk-stones, are composed of urate of soda, with traces of urate of lime. When in acute inflammatory disease, the uric acid is increased, the urea is simultaneously diminished. In diseases of debility, this acid is usually diminished in quantity; it may also be reduced by a spare diet, the avoidance of acids, the use of large quantities of water, open-air exercise, so as to ensure the perfect oxygenation of the blood, and by all measures tending to increase the action of the skin, such as exertion, friction, baths, especially hot-air and water baths, and warm climates. The use of tobacco augments its excretion, whilst quinine and alcohol lessen it. Alkalies assist in its excretion.

Hippuric acid (ἵππος, a horse), first detected in the urine of the horse, is also constantly present in human urine, sometimes amounting to as much as 15 grains in twenty-four hours; it has often been overlooked (Liebig). It crystallises in four-sided prisms, and has the atomic composition, $C_9H_9NO_3$, so that it is neither so nitrogenous nor so completely an oxidised body as urea or uric acid, but contains a larger proportion of carbon than either substance. Benzoic acid and other benzoyl compounds, also oil of bitter almonds, and succinic and other allied acids, when taken internally, cause an excess of hippuric acid in the urine (Ure). To explain this, it has been suggested that benzoic acid, $C_7H_6O_2$, combined with the bile product, glycocoll, $C_2H_5NO_2$, is equal to one atom of hippuric acid, and one atom of water. The source of the hippuric acid ordinarily present, is not yet known. Its quantity is influenced by the character of the diet, and by the amount of exercise; it is increased by a purely vegetable diet, is lessened by a mixed diet, and is diminished still more remarkably in

those who are living on animal food only. According to some, it is absent in persons who abstain from spices; also in infants at the breast, and in Herbivorous animals deprived of food. In the last two cases, uric acid alone is produced, in the one case, from the milk, and in the other, from the tissues of the animal itself (Ranke). Hippuric acid is not only found in large quantities in the horse, but also in other Herbivorous animals; and most of these consume grasses, in many species of which, certain aromatic principles exist. In the Carnivora, it exists in minute quantities. Although, most probably, hippuric acid is commonly derived from certain aromatic substances, yet it has been shown that its formation from albuminoid bodies, is quite possible (Städeler).

Very minute quantities of benzoic acid, and xanthin or xanthic oxide, also exist in the urine, with traces of certain volatile acids, phenylic, carbolic and taurilic, on which the odour of this fluid may depend.

The *creatin* and *creatinin* found in the urine, are both crystallisable nitrogenous bodies. The former exists in small quantities, the latter amounts to about 15 grains a day. Creatinin $C_4H_7N_3O + 2(HO)$, differs from creatin $C_4H_9N_3O_2$ by one atom of water. They are obtained by precipitation with salts of zinc, and by the subsequent decomposition of the zinc compounds. Creatin is a neutral substance, incapable of combining either with acids or alkalies; but creatinin is a powerful base, having a strong alkaline reaction, and forming crystallisable salts with acids. Creatin exists in large quantities in the juice of muscle, from which it was first prepared by Liebig. Creatinin is present only in small quantity in the juice of flesh, but is readily formed by the action of strong acids upon creatin. Creatin appears to be, with succinic acid, a product of the decomposition of syntonin, whilst creatinin results from still further decomposition; from its basic nature, it approaches in character to urea, into which substance, and sarcosin, it is decomposed by the action of baryta at the boiling-point. Albumen may be broken up artificially, by the action of powerful acids or alkalies, into glycocoll, tyrosin, and leucin, nitrogenous bodies intermediate between it and urea. By the action of caustic alkalies on creatin, urea is formed, whether through the previous formation of creatinin is not certain. Albumen, creatin, creatinin, and urea, form, therefore, a descending series of nitrogenous bodies. Both creatin and creatinin are more abundant in exercised muscles,

and, therefore, would seem to be products of muscular action; both substances are present, in small proportions, in healthy blood, from which they are excreted, also in small quantity, by the kidneys. They are supposed to be transformed chiefly into urea, probably through the agency of the epithelial cells of the uriniferous tubes, and, thus changed, finally enter the urine. Creatin and creatinin, therefore, are compounds probably preformed in the body, *i.e.* in the muscles, thence entering the blood by venous absorption; they are excreted from it, in minute quantity, in their proper form, but chiefly after conversion into urea. They are the principal immediate source of the last-named substance, which is even associated with them, in the juice of the flesh of certain Cartilaginous Fishes (Frerichs and Städeler).

The *colouring* substance of the urine, *urinary pigment* or uro-hæmatin, contains iron, and is separable into red, blue, and yellow colouring matters, named uro-rhodin, uro-glaucin, and uro-xanthin. Their nature is not well understood; they exist but in small quantity, and are very prone to decomposition. According to some, these pigments are allied to indigo, and its derivatives, indigo-red, indigo-blue, and indican. The blue pigment, or uro-cyanide, is named the indigo of urine.

The non-crystallisable extractive matters of the urine, exist in large quantities, and require further investigation; they are nitrogenous bodies, some even containing sulphur and phosphorus, probably derived from the albuminoid tissues; they are liable to decompose, and are abundant in certain diseased conditions.

Traces of mucus and epithelium, either of the spheroidal glandular kind from the tubuli, or of the squamous kind from the interior of the bladder, also occur, as cloudy deposits, in this excretion.

There are also several non-nitrogenous, hydro-carbonaceous, or carbonaceous substances in urine. Thus, *lactic acid*, $C_3H_6O_3$, occurs occasionally, as, *e.g.* when that acid, or some of its salts, are present in large quantity in the blood, owing to feeble conditions of the respiratory process, or to defective oxidating processes in the blood. By Lehmann, lactic acid is said to be constantly present, and to be the cause of the acidity of the urine; but, by others, this is supposed to depend upon free phosphoric acid, or, on an acid phosphate of soda, or perhaps upon this acid, together with a minute quantity

of dissolved uric acid ; for it is difficult to suppose the existence of free lactic acid, so long as any alkaline urates are present, and these latter salts may always be obtained by the quick evaporation, *in vacuo*, of perfectly fresh urine. The acidity of the urine, gradually diminishes for from three to five hours after a meal, and sometimes the excretion becomes actually alkaline. This effect occurs simultaneously with the development of the large quantity of acid in the gastric juice poured out for the digestion of the food ; whilst the return of the urine to its acid condition during fasting, corresponds with the cessation of the formation of acid in the stomach. This temporary diminution in the acidity of the urine, or its positive alkalinity, is most marked when animal food is taken, which requires more acid to digest it ; with vegetable food, it is less so ; with mixed diet, the effects are intermediate (Roberts). The alkalinity of the urine after a vegetable diet, and of that of the Herbivora generally, is not opposed to these observations, and has another explanation. In such diet, large quantities of neutral alkaline salts of the vegetable acids are met with, which are converted in the alimentary canal, or in the blood, into carbonates ; the quantity of albuminoid food or tissue metamorphosed, is so small, as not to yield enough sulphuric and phosphoric acid, to neutralise this alkali. The urine is also often alkaline in gastric disorder. In the Carnivora, ammonia acts the part of a base to the acids of the urine, instead of the fixed alkalies.

Oxalic acid, $C_2O_3 + H_2O$, also occurs in the urine, especially after eating fruit, which contains organic acids, also after drinking fluids containing free carbonic acid, and lastly, when the respiratory process is seriously disturbed. Any condition which tends to overload the blood with carbonic acid, favours the appearance of oxalic acid in the urine ; in children, it is a frequent constituent, and, in combination with lime, forms the comparatively common *mulberry calculus*. Lastly, *carbonic acid* itself is found in a state of solution, in the quite recently discharged urine of both Man and animals. Besides this, the urine contains nitrogen, with traces of oxygen, and, but only as a product of decomposition, sulphuretted hydrogen.

Minute traces of certain *fats*, such as olein and stearin, occur in urine. In certain cases, a fatty substance, probably a mixture of ordinary fats, named *keistin*, appears as a scum upon it ; and, in altered conditions of the kidneys, large quantities of oily matter, rise up to the surface.

The *salts* found in the urine, average about 1·8 part per cent. of that fluid, though they vary extremely according to the character of the food, and the amount of fluid ingesta; the latter increase their quantity. Of 100 parts of these salts, the sulphates form 45 parts, the phosphates 24, and the chlorides 23, the residue consisting of the salts of the organic acids. The chief base is soda, next in order potash, then ammonia, magnesia, lime, and lastly, in minute quantities, iron and silica. Whilst most of these salts are derived directly from the materials of the food, others undoubtedly proceed from the metamorphoses of the tissues; but even these are, of course, ultimately derived from the food. The sulphates and phosphates of the alkalis, originate in the oxidation of the sulphur and phosphorus belonging to the albuminoid substances found especially in the muscular and nervous tissues; the quantity of these salts, is increased by exercise, which conduces to changes in those tissues. The earthy phosphates must also be ultimately derived from the food, either directly, or through tissue changes; their quantity appears to increase, on the administration of chloride of sodium. The chloride of sodium itself varies in quantity, according to the amount consumed with the food; one office of the kidneys, is to regulate the quantity of that salt retained in the blood. The ammonia of healthy urine, occurs chiefly in the triple phosphate of ammonia and magnesia; it is an ultimate product of the decomposition of albuminoid substances, the creatin, creatinin and urea being probably intermediate stages.

Under certain circumstances, amorphous or crystallised deposits, or *sediments*, are formed in the urine; and sometimes, even solid concretions, named *urinary calculi* or *stones*, occur in it even within the body.

The most common sediment is of a *yellowish* or *reddish* hue, and consists of mixed *urates* and *uric acid*, with some of the colouring principles; these, being less soluble in cold than in hot fluids, may be precipitated from urine, clear at the time of its discharge from the body. When turbidity exists at the moment of discharge, or subsequently, though the urine be maintained at the temperature of the interior of the body, the condition must be regarded as one deviating from health. But a uric acid sediment may be caused by an acid fermentation of the urine, often associated with the growth of penicillium. The acid then formed, usually lactic acid, decomposes the urates in solution, and uniting with their base, whether soda

or ammonia, precipitates the less soluble uric acid. The coloured extractive matters may, through changes produced in them by atmospheric action, increase the solvent power of the fluid for the urates, and so prevent their precipitation in the process of cooling. The quantity of uric acid sediment, therefore, does not necessarily correspond with that in the urine itself, for sometimes it may be precipitated, though existing in small proportion, and sometimes be suspended, though present in larger quantity. If the uric acid compounds be in excess, the temperature lowered, and a free acid be formed, a deposit is sure to take place. In hot climates, the cutaneous excretion is very active, a quantity of acid is thus removed from the system, and deposits of lithic acid are accordingly rare. *Phosphatic* sediments are also occasionally met with, owing to peculiar decompositions or fermentations, affecting the urea, which is then converted into carbonate of ammonia; by this, the earthy phosphates are precipitated, as ammoniacal magnesian phosphate, or as phosphate of lime. This alkaline fermentation occurs sooner or later, at certain temperatures; but in those diseases, in which the urine is too long retained in that viscus, and also in inflammation of the urinary mucous membrane, it sometimes happens in the bladder itself. This form of alkalinity is to be distinguished from that which depends on the presence of potash or soda; in the latter case, the blue colour given to litmus paper, is permanent; whilst with ammoniacal urine, it is fugitive, owing to the volatility of ammonia. The alkaline fermentation is probably induced by the pus, or by the excess of mucus. The acid fermentation is also believed to be excited by the mucus of the bladder. The abundant sediments formed in the critical stages of fevers and gout, are of the uric acid type. The fine iridescent film, frequently seen on the surface of the urine, in dyspeptic and nervous diseases, consists of crystals of the triple phosphate of ammonia and magnesia. Prolonged mental effort is said to cause an increase in the amount of phosphates; but this is not established by observation, although this condition does occur in diseases of the nervous centres. The known existence of phosphorus in the fatty matter of the brain, has doubtless suggested this idea. Other morbid sediments consist of pus and blood.

The concrete deposits named *calculi*, commence by the collection of some crystallisable substance, around accidental fibrinous or other masses which may be minute, and ultimately

almost, or entirely, disappear. Upon such a centre of formation or *nucleus*, successive layers of crystallised substance are deposited in laminae or crusts, cemented together by traces of mucus. The first layers deposited, often differ from those which follow, and sometimes the layers alternate, constituting a *composite* calculus. The simplest calculi are those consisting of a mixture of uric acid with urates, forming the *uric* or *lithic acid* group; they are generally oval, somewhat flattened, smooth, or slightly rough, yellowish, and hard. The *oxalate of lime* or mulberry calculi are, as their name implies, roughly tuberculated, and brownish or black in colour; they are very hard. They contain some colouring substance derived from the blood. The *phosphatic* calculi are either smooth on the surface, opaque-white, or white and semi-transparent, or else finely crystalline, light and soft, so as, indeed, to be easily worn by attrition, when two or more coexist in the bladder; they offer but little resistance to crushing instruments. They are composed of the triple phosphate of ammonia and magnesia, combined with some phosphate of lime. Other and rarer forms of urinary concretions, are the *carbonate of lime*, *cystic oxide*, and *xanthic oxide* calculi.

Many articles of diet, and medicinal agents, pass into the urine entirely *unchanged*; such are the alkaline chlorides, phosphates, sulphates, and nitrates. Of these salts, chloride of sodium acts especially as a stimulant to all the processes of tissue metamorphosis, and herein may be found one of the chief uses of this universal constituent in the fluids of all animals. The carbonates of the alkalies, and the caustic alkalies, produce, however, still more powerful effects. The vegetable alkaloids, as quinine, morphia, and strychnia, certain vegetable colouring substances, such as saffron and rhubarb, and many odorous substances, as turpentine, garlic, assafoetida, and valerian, likewise pass unchanged. Nitric, phosphoric, and sulphuric acids also escape, combined with appropriate bases derived from the blood; sulphuric acid displaces phosphoric, and this latter acid, the feeble inorganic and organic acids. Most substances, however, undergo a *change* before they enter the urine. Thus, the organic acids, such as lactic, but especially tartaric, citric, malic, racemic, and also acetic acid, and their salts, do not reach the urine as such, but, united with soda or potash, they are converted in the system, into carbonates, which enter the urine. Hence, the alkaline condition of this fluid, caused by succulent vegetable diet, and

the alkaline urine of the Herbivora. Again, as already mentioned, benzoic acid and the allied cinnamic acid, are first converted into hippuric acid. Organic compounds containing sulphur, produce sulphates in the urine. A great number of substances, on being taken into the stomach, do not reappear in the urine, such as ether, thein, caffen, theobromin, asparagin, amygdalin, musk, camphor, and certain colouring matters, such as cochineal and chlorophyll. Alcohol, though chiefly decomposed in the system, may partly appear in the urine. Of the metallic salts, such as arsenic and antimony, the bases of which can, of course, undergo no change in the body, some appear with great facility in the urine; whilst others enter that fluid with difficulty, or only in minute traces even after long periods of administration; such are gold, silver, mercury, lead, bismuth, zinc, and iron. Alumina is absorbed with difficulty, or not at all, hence it does not appear in the urine.

Water is eliminated with great rapidity from the kidneys. In large quantities, as already stated, it causes, by stimulating the excreting power of the uriniferous tubes, an absolute increase in the amount of urea separated from the body; though relatively, owing to its dilution, a given quantity of urine contains less urea. The diminution in the quantity of urea and uric acid excreted by the kidneys, caused by many agents, such as coffee, tea, alcohol, and tobacco, articles so widely and instinctively adopted by mankind as dietetic substances, has been explained, by supposing that they interfere with, or retard, the metamorphoses of the albuminoid and fatty tissues, and so preserve them from waste. In this way, when taken in moderation, they conserve the strength. The action of creatin and creatinin, so abundant in beef-tea and beef-juice, may be similar. Thein and caffen resemble those substances very closely in composition.

The *rapidity* with which water and substances soluble in it, pass into the urine, after being taken into the stomach, formerly led to the idea, that direct channels of communication, passages, or ducts, existed between the stomach and the kidneys, or some other part of the urinary apparatus. Many investigations were undertaken, some even with pretended success, for the purpose of discovering such passages. No such communications, however, exist. Soluble substances pass from the stomach into the circulation, by venous absorption, and are then, after traversing the lungs, conveyed by the renal

arteries to the kidneys, in which, by porous diffusion or dialysis, they enter the uriniferous tubules, and so reach the urinary passages. The rate at which this circuitous route through the vascular system, from the stomach to the kidneys, occurs, is adduced as one proof of the rapidity of the circulation of the blood (p. 170). When the stomach is empty, after long abstinence, the time is 1 minute; 4 hours after a meal, it is 2 minutes; $1\frac{1}{2}$ hour after, $6\frac{1}{2}$ minutes; 1 hour after, 14 minutes; and 25 minutes after, 16 minutes. If the test substance be taken with the food, it requires 40 minutes for it to appear in the urine (Erichsen).

The affinity of certain substances for the living tissues, influences the rate of their passage from the stomach to the kidneys, saline substances, for example, passing more rapidly than colouring matters. The relative diffusibility of the substances, may also modify the result. Pigments pass but slowly, indigo and madder requiring fifteen minutes, rhubarb and biliary pigments twenty minutes, logwood and other colouring matters, twenty-five minutes.

It has been seen that many substances, which are formed in, or belong to, the body, are liable to enter the urine, viz. pus, fatty matters, certain biliary products, sugar, inosite, leucin, allantoin, tyrosin, sarcin, hæmatin, fibrin, and albumen. If *bile* be no longer separated from the blood in the liver, or if its discharge by the alimentary canal, be prevented, it may appear in the urine, as it will in any other secretion or excretion; this happens in certain organic diseases of the liver. But, in the more common form of jaundice, the bile pigments *only* pass into the urine, giving it a dark colour. The *sugar* which appears in the urine in diabetes (p. 340), is not produced in the kidneys, nor does its presence in the urine necessarily imply disease of those organs; a larger quantity than usual being present in the blood, it escapes through the excreting structure of the kidneys. Its increased amount in the blood, depends on an abnormal action of the liver, or on the imperfect oxidation of the sugar in the blood, through some defect in the respiratory process. The transitory appearance of sugar in the urine, is not of much consequence; but its persistence in diabetes, is serious. A minute trace constantly occurs in healthy urine, though it escapes ordinary tests (Brücke). The presence of albumen in the urine, is important, especially if persistent. If temporary, it indicates pressure, or a great attenuation, of the blood, or else an increased pressure on the

blood in the renal arteries. Thus, drinking enormous quantities of water, has been known to produce temporary albuminuria or albuminous urine; on the other hand, albumen is sometimes met with in this fluid, after indulgence in very full meals, or in cases where the heart's action is materially increased, or again, where the aorta is compressed below the renal arteries, or from renal congestion or inflammation produced either by cold applied to the skin, or by the undue use of diuretics or irritants, such as the Spanish fly; possibly, also, by division of the renal sympathetic nerves (Krimer). The occurrence of albuminoid matter after full meals, may be accounted for, by the probable introduction into the blood, under those circumstances, of more or less albuminose, which has a higher osmotic tendency than albumen itself; when injected into the veins, it, indeed, appears in the urine. Again, ligature of the aorta below the renal arteries, in animals, or the forcible injection of blood through those vessels, causes an artificial albuminuria. Persistent albuminous urine indicates some degeneration of the excreting tissues of the kidneys, usually consisting of the so-called granular degeneration, or "Bright's disease," the result of interstitial deposits of an albuminoid, fatty, or amyloid nature. In such cases, the lateral pressure of the blood in the capillary vessels of the kidneys, is increased, either by the obstruction of the circulation through them, or as a result of the non-performance of the ordinary excreting process. Besides the albumen of the blood, even the plastic fibrinous substance may exude into the uriniferous tubules, and, becoming coagulated in their interior, form, together with altered epithelial cells, or with fatty matter, uric acid, blood or pus corpuscles, little cylindrical masses, known as *casts*, which are washed out of the tubes, and are easily detected in the urine by the microscope. Sometimes, the casts consist only of basement membrane. Bright's disease may, however, exist without the presence of albumen, in the urine.

To detect bile in the urine, Pettenkofer's test is used (p. 76). Sugar is detected by Trommer's copper test (p. 85), or by boiling with liquor potassæ, which causes a deep brown colour when sugar is present. Albumen is detected by boiling the urine, and adding a few drops of nitric acid, to make sure that the urine is not alkaline; certain precipitates, caused by heat, are then dissolved, but an albuminous precipitate remains, as whitish or yellowish flocculi of coagulated albumen. After

the continued administration of certain metallic poisons, such as arsenic and antimony, their detection in the kidneys or liver, may furnish the means of discovering crime.

As the blood is the most complex fluid proper to the body, being the source of nourishment to the tissues, and also the medium through which the products of their metamorphoses reach the excreting glands, so the urine is by far the most complex of the animal excretions. Its peculiar ingredients display important relations to the gelatinoid and albuminoid principles of the body and of the food, the metamorphoses of which, during the nutrition of the muscular and nervous systems, constitute, with those of the hydrocarbons and carbohydrates consumed in respiration and motion, the characteristic chemical phenomena of animal life. They especially eliminate nitrogen, but also a large amount of carbon, and some hydrogen. The excretion of effete nitrogenous matters by the kidneys, may be assisted by the liver; but most of the nitrogenous fatty acids of the bile, are reabsorbed. It is by the kidneys, that these nitrogenous products of metamorphosis, are constantly being removed; and if their function be arrested, grave mischief ensues. Ligature of the ureters is followed by an accumulation of urea in the blood; removal of the kidneys, by an increase of the creatin and creatinin in the blood, and also, though to a less extent, of urea, which is found in the serum; a urinous odour appears in many of the secretions. In the uræmic poisoning, which depends on disease of the kidneys, the urea, ceasing to be excreted through them, is detectible, in large quantities, in the perspiration, and also in the vomited matters. The urea itself, or the carbonate of ammonia resulting from its decomposition, then easily detected in the breath, circulates through the brain and spinal cord, and causes imperfect respiration, convulsions, coma, and death.

The Kidneys and the Urine in Animals.

These important glands, so essential to the animal economy, are well developed in all the Vertebrata, forming, as in Man, two symmetrical organs situated at the back of the abdomen. In Mammalia, as in Man, the kidneys are composed of an external cortical substance, consisting chiefly of convoluted tubuli, and of an internal medullary substance in which the tubuli are straight. The kidneys of many Mammalia exhibit the typical bean shape, but they are often more rounded than in Man, as in the sheep, pig, and dog. They are sometimes more or less lobulated. In the ox, the kidney is sublobulated, being marked by fissures between the pyramids, which form the lobules, remaining, however, united beneath

the divided cortical portion. In certain Carnivora, as in otters, seals, and bears, the pyramids, each covered by its own cortical layer, are separated by deeper fissures, into which even the capsule of the kidney penetrates, so that the lobules form clusters of distinct polyhedral masses attached to the separate infundibula of a much ramified ureter. The kidney is most deeply lobulated in the Cetacea. In the early embryonic condition of this organ in all Mammalia, the lobulated character is present; in the Cetacea and certain Carnivora, it persists, and forms the so-called compound kidney; in other animals, as in the ox, the lobules partly coalesce; lastly, in the sheep, dog, and Man, they completely unite, as development advances. Indeed, a lobulated or ramified condition seems to be a less developed form of many glands than the massive shape, as is illustrated by the liver, pancreas, spleen, and thymus in animals. Lobulation of the lung, however, is a sign of higher development. Subordinate peculiarities exist as to the mode in which the papillæ of the kidneys, are connected with a simple or much subdivided ureter.

In *Birds*, the kidneys no longer present an obvious distinction into a cortical and medullary substance, and the gland tissue is much less firm than in the Mammalia. In Birds, these organs are of considerable length, occasionally blended together, in places, across the middle line; they extend from the posterior border of the lungs, down to the lower end of the rectum, and are moulded into recesses in the bones of the lower part of the spinal column. The kidneys of Birds are, therefore, slightly lobulated. The uriniferous tubuli of each lobule, are arranged in bundles or tufts, which end in the outer or superficial part, by dichotomous tubes; the symmetrical ureters proceed from the abdominal surface of the glands, receiving the uriniferous tubules directly, without the formation of infundibula, or of a pelvis. They open below, in the upper and back part of a dilatation found at the lower end of the alimentary canal, named the cloaca, where there is a sort of recess, which has been regarded as representing an imperfect bladder.

In *Reptiles*, the kidneys are very large, occupy the same general position as in Birds, and are usually of great length. In the turtles, tortoises, and lizards, they are symmetrical, and fixed to the lumbar and pelvic regions; but in Serpents, the right kidney is placed higher than the left, as if for convenience; they extend along the greater part of their elongated and flexible spine. The kidneys present no distinction of cortical and medullary substance; but they are deeply lobulated, and loosely connected with the surrounding parts. The ureters are long and narrow, and end in a sort of cloaca. The *tubuli uriniferi* are reduced to convoluted, or even short straight, cæcal tubes, arranged in converging bundles, or placed transversely. In the crocodile, the convoluted tubuli are so distinct as to appear like a cortical layer.

In *Amphibia*, the kidneys are flat and broad at their hinder end, but become very narrow at their anterior part, and thus show an approximation to their form in Fishes. Numerous ducts proceed from their inner border, to a long slender ureter, which opens into the cloaca.

In *Fishes*, the kidneys are proportionally large; they vary in shape in different species, but, as a rule, are narrow and of extreme length, being attached beneath the bodies of the vertebræ, along the whole or the greater part of the abdominal cavity, above the air-bladder when that organ exists. There is no distinction of cortical and medullary sub-

stance, and tufts of slightly tortuous urinary tubuli, or completely straight cæcal tubes, end at once in narrow elongated ureters, which usually open, on each side, into the cloacal portion of the rectum, but which sometimes first coalesce. In the low Myxinoid fishes, the upper portion of the kidneys is much attenuated, and presents a complete unfolding of the gland structure; the tubuli, instead of being long and aggregated, are short, distinct, and commence by little dilatations, into which the Malpighian glomeruli project. In the amphioxus, the kidney has not been distinctly made out, though it is probably represented by a narrow gland-like mass placed near the abdominal pore.

The kidneys in Birds, Reptiles, Amphibia, and Fishes, may be considered as composed entirely of cortical substance; they invariably contain Malpighian corpuscles, or arterial glomeruli, which are usually scattered through the gland, and, as usual, project into dilatations of the uriniferous tubuli. These bodies vary in size, apparently in accordance with the size of the animal, as well as in different Classes. Thus they are larger, $\frac{1}{70}$ and $\frac{1}{80}$ of an inch in the lion and horse, than in Man, $\frac{1}{100}$; they are much smaller in the guinea-pig, cat, and mouse, $\frac{1}{200}$ to $\frac{1}{250}$ of an inch; they are small in Fishes, $\frac{1}{200}$, and Amphibia, $\frac{1}{250}$, but smallest of all in Reptiles, $\frac{1}{240}$ to $\frac{1}{400}$. In the pointed renal lobules of the boa, they are smaller in the narrow than in the wider portions of each lobule. In the simpler kidneys of Fishes, they are represented by small vascular plexuses. Cilia are found in the uriniferous tubuli in the Cold-blooded Vertebrata; they commence at the neck of the capsules into which the Malpighian bodies project, and extend for a short distance along the tubuli, sometimes throughout their whole length. The current which they produce, as seen after death, is towards the orifices of the tubules. Cilia have not yet been distinctly seen in Birds or Mammalia.

In Birds, Reptiles, Amphibia, and Fishes, the renal arteries, instead of being two in number as in Mammalia, are numerous, and are derived from adjacent branches of the aorta, or from the aorta itself. Besides this, the kidneys in these Classes, receive more or less venous blood from the hinder limbs in Birds and the four-footed Reptiles and Amphibia, and from the hinder parts of the body in Ophidia, and in Fishes. The rest of the blood from the hinder portion of the body, usually passes partly to the vena cava, and partly to the vena portæ; in Reptiles, Amphibia, and most Fishes, it goes chiefly to the latter; in a few Fishes all the blood from the hinder part of the body, proceeds to the kidneys.

The fact, that the kidneys in Birds, Reptiles, Amphibia, and Fishes, receive a supply of venous blood, was first noticed by Bojanus, but the detailed arrangement of the afferent veins was fully investigated by Jacobson. These renal portal veins become more numerous in the lower Vertebrata. After entering the kidneys, they quickly subdivide, and end in the vascular plexuses which surround the uriniferous tubuli. The Malpighian bodies still receive arterial vessels only, but give off efferent vessels which join the plexuses around the tubuli. In the lower Vertebrata, accordingly, the special urinary products, like the bile products, are, in all cases, excreted from venous blood; and the small quantity of arterial blood which enters the kidneys, first passes through the vascular tufts of the Malpighian bodies, and so becomes modified, before it reaches the plexuses around the proper excreting tubuli, in the same manner that the hepatic arterial blood becomes venous, before it reaches

the intra-lobular plexuses of the liver. As already stated, the existence of this portal arrangement of the vessels in the kidneys of Birds, Reptiles, Amphibia, and Fishes, supports the view, that in Mammalia, also, the renal arterial blood becomes venous in traversing the vessels of the glomeruli, before it serves for the excretion of urinary constituents. The pasty or solid character of the urine in Serpents, may depend, not only on the small size of the glomeruli, but also on the fact, that these animals swallow little or no water.

Excretory glandular organs, having the function of kidneys, exist at least in the higher Non-vertebrate animals; but owing to the different plans of construction in these Sub-kingdoms, it is impossible to recognise much, if any, resemblance of position or structure, between them and the renal organs even of the lowest Fishes. But the unity of the vitæ-chemical processes of animal life, is proved by the detection of urinary products in some of these excretory organs in the Mollusca, Annulosa, and Coelenterata. Uric acid has been found in the two former Classes, and guanin in the last.

In the *Mollusca*, the organs which represent kidneys, are not connected by ducts, with the alimentary canal. In the Cephalopods, remarkable spongy masses of follicles, exist around the large branchial veins, and discharge themselves, by numerous apertures, into the branchial cavity: these are supposed to act as renal emunctory organs, their excreted fluid containing uric acid. In the Gasteropods, a smaller follicular organ, also containing that acid, is usually found in the neighbourhood of the heart, and its ducts open near the intestinal orifice, generally into the branchial cavity. In the Lamellibranchiata, a similar organ, but, in most cases, less distinct, is also found near the heart, close to the lower end of the intestine, opening into the cavity of the mantle. In the *Molluscoïda*, distinct renal organs have not yet been recognised. Amongst the *Annulosa*, the *Insecta*, *Myriapoda*, and *Arachnida*, have excretory organs believed to be renal, consisting of long tubes, often beginning by clusters or tufts of vesicles; they are sometimes few, as in *Myriapoda*, sometimes very numerous, as in the higher *Insects*. As in the *Vertebrata*, they open into the lower part of the intestine, or even close to its orifice; sometimes the principal duct is dilated near its lower end, as if to form a urinary bladder. The coloured fluid discharged by the lepidoptera, on their emerging from the chrysalis, proceeds from these vessels, and contains uric acid. No such renal organs are found in the *Crustacea*, which are aquatic. In the *Annuloida*, in which they are likewise absent, the water-vessels may have some excretory function, and eliminate urinary products.

In certain of the *Coelenterata*, small clusters of cells projecting into the body cavity, and containing guanin, are regarded as renal organs; but in the simplest forms of these animals, the excretion of the products of the decomposition of albuminoid substance, is probably accomplished by the external and internal surfaces of their hollow bodies.

Lastly, in the minute *Protozoa*, such products must also be eliminated by the general surface.

Special Secretions in Animals.

Certain secretions or excretions, in animals, may perhaps be regarded, not merely as serving a peculiar purpose in the economy, but also as fulfilling an emunctory office, eliminating from the system, substances which might be as injurious to animal life, as urea and uric acid. Amongst such, may be mentioned, the castor of the beaver, the musk of the musk-deer, the peculiar secretion of the civet-cat, and those of other Mammalia, also the venom of Serpents, the acrid secretion of the skin of the toad, the ink of the cuttle-fish, which yields the sepia colour used by painters, the poisons of the stings of the bee and the wasp, the sugar secreted by aphides, the odoriferous excretions of the bugs and many other beetles, the poison in the tail of the scorpion and the mandibles of the spider, the odoriferous exudations of the lumbrici, and even the threads of the sea-nettles. Examples of special secretion, are also met with in those glands which, in many caterpillars, supply the silk used in progression or for the cocoons, in the spinneret glands of the Spiders, the cement gland of the Cirrhopods, and the glandular structures which secrete the byssus of certain Lamellibranchiata.

However different and specialised may be the actions of the various glandular organs in the Animal Kingdom, which yield such widely different products, they are all based on a common plan of structure and function. Even in the highest animals, and in Man, their physiological relationship is evidenced by an occasional tendency to a vicarious action, in which one gland or several glands take on the suspended function of another.

THE SKIN AND ITS EXCRETIONS.

By means of its sebaceous and sudoriferous glands, the skin secretes and excretes fatty matter, and the perspiration or sweat. Besides this, it exhales water from its surface, and throws off certain quantities of carbonic acid gas.

The *sebaceous* or *oily matter*, formed by the so-called sebaceous glands (vol. i. p. 459; fig. 69, *a*), consists of a mixture of olein, saponified fat, cholesterin, a small quantity of an unnamed albuminoid substance, and a few epidermic cells. Its ashes abound in earthy phosphates. The fat is either derived from the fatty matter of the plasma of the blood, or more probably from the metamorphosis of the albuminoid contents of the epidermic cells of the sebaceous glands. It is poured out, partly on the surface of the skin, but more commonly into the interior of the hair follicles, even into the most minute ones. It contributes to soften and render flexible both the hairs and the skin, and, by protecting the latter from the action of water or aqueous solutions, it renders the skin more effectual as a defensive organ. The so-called *ceruminous* and *Meibomian*

glands of the ear and eyelids, may be regarded as special modifications of sebaceous follicles.

In all Quadrupeds which possess hairs, sebaceous or oil glands exist; the *glandulæ Uropygii*, or caudal glands, of Birds, supplying the fatty secretion with which they anoint their feathers, are highly developed sebaceous glands.

The epidermic tissues generally, viz. the cuticle, nails, and hairs, have been viewed as solid excreted substances. When worn, cut, shed, or desquamated, they undoubtedly rid the economy of a large amount of nitrogenous, sulphurous, and ferruginous matter. The continual loosening of epithelial cells, from the gastro-pulmonary cavities, must serve a similar office.

The *sudoriferous*, *sudoriparous*, or *sweat glands* are present, in larger or smaller numbers, in all parts of the skin. They are small, rounded, pinkish bodies, placed immediately beneath the true skin, and average about $\frac{1}{6}$ of a line in diameter. Each sweat gland consists of a fine tube, closed and coiled up into a ball at its deeper end, from which a straight part of the tube, or duct, passes up through the cutis and cuticle, and opens by a somewhat widened orifice on the surface. When the cuticle is thick, as in the palms and soles, this tube passes through it in a spiral manner (fig. 66, 5, 6). The whole tube, when unrolled, measures about $\frac{1}{4}$ of an inch in length, and about $\frac{1}{300}$ of an inch in width. This tube consists of an outer vascular coat, prolonged from the cutis, and of an epidermoid lining, continuous with the cuticle; the spiral portion is composed of the latter only. Two coiled tubes may unite into one duct. When a sweat gland is destroyed, it is not reproduced. In some situations, the sweat glands are of large size, as in the axillæ, where they measure nearly two lines in diameter, are of a darker red colour, are composed of branched tubes, and secrete a thick, exceedingly acrid, and odorous fluid. In the palms and soles, the openings of the sweat glands, the so-called *pores* of the skin, are found on the papillary ridges; in other parts, they are scattered over the surface. They are most numerous on the palm of the hand, where 2,800 orifices are found on a square inch; they are fewest on the back of the neck and trunk. Non-striated muscular fibres, arranged longitudinally, exist in the vascular coat of the ducts of the larger sweat glands (Kölliker).

The *perspiration*, or *sweat*, which is excreted by the *sudoriferous* or *sudatory* glands, is not the only watery exhalation from the skin; for water is undoubtedly exhaled from the in-

tegument generally, as well as from the sweat glands. The perspiration is said to be *insensible*, when no visible moisture is discernible on the skin, and *sensible*, when it is so discernible; but there is no real difference between them; in the former case, the fluid part evaporates as fast as it exudes from the orifices of the sweat glands, whilst, in the latter, it remains for a moment or so, in minute transparent colourless drops.

The sweat usually contains about 97·5 of water and 2·5 of solid matter, but sometimes less than 1 per cent. of the latter. The organic constituents are little more than half of this, and are composed chiefly of fat, which is probably almost entirely derived from an admixture of the secretion of the sebaceous glands; but the palms of the hands and the soles of the feet, are more or less greasy, although no sebaceous follicles exist in that part of the skin. Besides this, the organic matters of the perspiration, contain an albuminoid substance, the nature of which is unknown, and acids, which give it an acid reaction, by some supposed to be lactic acid, but now usually regarded as a mixture of a peculiar nitrogenous acid, named *sudoric*, with the volatile acetic, metacetic, formic, and butyric acids, together with the fatty caprylic and caproic acids. Some of these acids are combined with alkalies. Almost one-fourth of the solid matter, is urea, the total daily quantity having been estimated at about 150 grains, which would yield about seventy grains of nitrogen. This urea is easily decomposed, and gives rise to ammoniacal salts, such as were described by Berzelius, for no ammonia is found in perfectly fresh perspiration. The inorganic matters are chiefly common salt and chloride of potassium, phosphate of soda, and traces of earthy phosphates, and iron. On burning the total solids, some sulphates are formed, indicating the presence of sulphur in some combination, probably with the organic matter. A certain quantity of epidermic cells and extraneous substances, also occur in the residue. The odour of the perspiration, depends partly on the volatile acetic, formic, and various fatty acids, but also perhaps on special, but unknown, volatile odorous substances. Some of the odour may be due to decomposing urea. In certain diseases, in which the excretion from the kidneys is seriously diminished, or altogether suppressed, as in Bright's disease and cholera, when the urea and uric acid are retained in the blood, large quantities are frequently excreted by the skin, probably chiefly by the sudoriferous glands. Besides the above-named substances, alcohol in small quantity,

sugar, albumen, biliary matters, and other substances, have been found in the perspiration.

The *uses* of the perspiration are two-fold; first, to get rid of a certain quantity of water from the system; and secondly, to eliminate from the body, certain special products of chemical metamorphosis.

Many attempts have been made to determine the average quantity of fluid exhaled by the skin, under ordinary circumstances, in twenty-four hours, and the variable quantities which are given off under different conditions. In the earlier experiments, the losses, by exhalation both from the skin and the lungs, were confounded, the body being weighed together with the food and drink taken in twenty-four hours; at the end of that time, the weight of the body was again taken, and also that of the intestinal and renal excreta; the difference in these two totals, gave, for the amount of cutaneous and pulmonary exhalation together, $\frac{5}{8}$ of the total loss of weight of the body (Santorini). By enveloping the body in an impermeable oil-silk bag, so as to condense and retain the water of the cutaneous exhalation, it was found that, in an adult, about 30 oz. are daily exhaled by the skin, whilst at the same time, 15 oz. are given off by the lungs, making a total daily loss, by both skin and lungs, of 45 oz. (Seguin). The total loss has, however, been estimated at $45\frac{1}{2}$ oz. in the autumn, 44 oz. in summer, and 37 oz. in spring, in a person under the average size (Dr. Dalton). Other estimates give an average total loss of 57 oz., 51 oz. in the winter, and 63 oz. in the summer.

The quantity of perspiration exhaled by different parts of the body, differs widely. Its general quantity is influenced both by intrinsic and extrinsic conditions; thus it is augmented by increased vascularity of the skin, by a higher temperature of the body, by a quicker circulation, and therefore by exercise and effort generally. Perspiration may also be induced by additions to the clothing or covering of the body, and likewise by breathing in a confined space; it is also increased by peculiar conditions of the nervous system, as by certain depressing emotions, and syncope, all of which tend to relax the skin and its bloodvessels. It is, on the other hand, diminished or almost entirely arrested, in febrile conditions and certain forms of excitement, and, it is said, also by the use of coffee. It is increased by taking food generally, but more particularly after dinner. The secretion is stated to be most active about

noon, and least so in early morning. It is also augmented during sleep.

Of the external conditions which modify the quantity of the perspiration, by far the most important are the temperature and hygrometric condition of the atmosphere. Thus in warm air, which increases the activity of the cutaneous circulation, the perspiration is increased, whilst cold air has the opposite effect; again, dry air increases the perspiration, whilst damp air diminishes it. Simple warmth acts by increasing the vascular action through the skin; whilst dryness operates by maintaining a constant evaporation from the cutaneous surface; on the other hand, cold diminishes the vascularity of the skin, and dampness of the air impedes evaporation. The combination of moisture with heat, however, increases the exhalation by the skin, which then appears in large drops. Motion in the air, whether warm or cold, dry or moist, increases the relative amount of perspiration, by carrying it off more quickly. The perspiration is said to be diminished by increased atmospheric pressure. This excretion is also augmented by large quantities of drinks, especially when taken warm; by so-called sudorific medicines, such as nitre, Dover's powder, and vinegar; by electricity; and also by hot baths, whether water-baths, vapour-baths, or hot-air baths, especially when, as in the Turkish and Roman baths, friction and shampooing are superadded. Certain curious local sweatings have been noticed, affecting the head alone, or the feet and hands, or even one side of the face only, phenomena which probably are due to some loss of power in the vasi-motor nerves of the arteries of those parts, giving rise to dilatation of the vessels, increased vascularity, and increased secretion. Suppression of the cutaneous exhalation and excretion, is more or less dangerous, causing either local internal congestion or inflammation, or general poisoning of the blood and fever, from the retention of effete matters in the system. Hence the ill effects of sudden cold, or chill to the surface, especially after previous overheating of the body to the point of fatigue, and with the accumulation of effete substances of waste in it. The chief use of this copious exhalation of water from the skin, as will be explained in the Section on Animal Heat, is that of regulating the temperature of the body, under variations of external temperature.

The mutual balance between the respective quantities of the renal and cutaneous exhalations, under different physical

conditions, chiefly those relating to the temperature and hygrometric condition of the air, is shown by the facts, that in cold weather the skin exhales less, and the kidneys excrete more fluid, whilst in warm weather the skin eliminates more and the kidneys less. The skin is sometimes said to regulate the quantity of fluid given off by the kidneys, and the quantity of fluid left, in reserve, in the blood and the soft tissues generally; but the kidneys should rather be regarded as the true regulators in this matter. The skin and also the lungs are exposed to external influences of temperature, and to the relative hygrometric state of the air, which must affect the quantity of their exhalations; but the kidneys, being placed in uniform conditions, are sensitive self-acting regulators, operating through stimulation of the vasi-motor nerves, which govern the state of the arteries and vessels of the glomeruli, and determine the supply of blood. In certain conditions, moreover, the renal and cutaneous excretions, instead of being vicarious as to quantity, are simultaneously increased or diminished.

The office of the perspiration, in removing effete matter from the blood, is, in the first place, evident, from the composition of its solid constituents, although these are comparatively scanty. Supposing 30 oz. of perspiration to be the daily quantity excreted, the amount of urea and of other peculiar solids thus eliminated, would be about $\frac{1}{3}$ oz.; whilst the daily quantity of solid urinary products amounts to from 2 oz. to $3\frac{1}{2}$ oz.

As an organ of excretion, however, the skin further eliminates carbonic acid gas. The skin, indeed, is to a slight extent, even in Man, a respiratory membrane, giving off carbonic acid, and actually absorbing oxygen. The quantity of carbonic acid gas exhaled by the comparatively dry cutaneous surface of the human body, is, of course, relatively to that given off by the lungs, very much less, and has been variously estimated at from $\frac{1}{30}$ to $\frac{1}{60}$ (Scharling), at $\frac{1}{35}$ (Scharling and Hannover), and at $\frac{1}{100}$ (Edward Smith), of that given off by the proper respiratory organs, the lungs. It is stated that in regard to the skin, a little more carbonic acid is given off than oxygen is absorbed, which is the reverse of what happens in the lungs; but the estimation of the quantity of oxygen absorbed, is extremely difficult. The same remark applies to the nitrogen, a minute trace of which is said also to be taken up by the skin. The activity of this cutaneous respiratory process, as it must be called, is considerably increased by exercise. The quantity of nitrogenous matter daily removed in

the shape of desquamated epidermic cells, is said to be about 11 grains. A partial interference with the excretory function of the skin, causes headache, lassitude, and febrile reaction; a more serious disturbance, by over-exciting the kidneys, will bring on temporary albuminuria.

The preceding facts sufficiently explain the high importance of cleanliness of the skin, for the preservation, not only of comfort, but of health. Daily ablutions by sponging, and the occasional use of the tepid bath, are of great efficacy in the maintenance of a pure condition of the blood.

The Cutaneous Excretion in Animals.

The sudoriferous glands of the higher Vertebrata, and the cutaneous glandular organs of the lower Vertebrate, and Non-vertebrate animals, have been already described (vol. i. p. 473).

When the skin of a rabbit is shaved, and the body subsequently coated over with varnish impenetrable to water and gases, death ensues from asphyxia in from six to twelve hours, a condition which has been named *cutaneous asphyxia*. The symptoms are depression, difficulty of breathing, lowering of the temperature, congestion of the tissues and organs with dark blood, and ultimate death. The arrest of cutaneous respiration may partly account for this form of death, with accumulation of carbonic acid in the blood; but doubtless also, it depends on the shutting in of peculiar cutaneous products. The fatal result can scarcely be referred to the non-exhalation of water. In the soft-skinned Amphibia, the entire cutaneous surface exhales carbonic acid, and absorbs oxygen; in the frog, for example, after removal of the lungs, $\frac{1}{4}$ cubic inch of carbonic acid gas has been excreted from the skin, in eight hours (Bischoff). This experiment is performed by putting the animal, after deprivation of its lungs, under a glass receiver filled with air, and placed over mercury; the carbonic acid is absorbed by lime water, and so measured. The skin of the frog, which is moist and full of capillary vessels, presents conditions favourable to the solution and diffusion of gases in contact with it, by a mechanism to be explained in the next Section. Probably nearly as much carbonic acid is eliminated by the frog, from its cutaneous surface, as from its comparatively simple lungs.

In the soft-skinned, aquatic, Non-vertebrate animals, the integument is often an adjuvant, or the chief, or sole, respiratory surface, being for that purpose frequently ciliated.

RESPIRATION.

The *arterial* blood in passing through the systemic capillaries, serves the purposes of nutrition, stimulation, secretion, and excretion, and the blood, as it leaves those capillaries,

is tainted by the products of venous absorption. In the various changes which it undergoes, the arterial blood both loses and acquires certain substances, and so becomes *venous*. Thus changed, it returns to the heart, and, being now conveyed through the pulmonary capillaries, is there rapidly restored to its arterial condition. This conversion of venous into arterial blood, is the *immediate* object of the respiratory process. In it, oxygen is absorbed by the blood, whilst carbonic acid, together with some watery vapour, is given off. The source of the oxygen is the atmosphere; the carbon of the carbonic acid is derived from the blood and tissues, themselves supplied by the food. The chemical union of the oxygen with carbon, and also with hydrogen, in the system, maintains the movements and the temperature of the body, and is the source of its nervous power and electricity.

The function of *respiration*, therefore, has for its immediate effect, the purification of the blood, and for its ultimate uses, the production of Animal Heat, Motion, and Nervous Energy.

In plants, as elsewhere mentioned, the respiratory process is reversed. Under the action of light, the carbonic acid and water taken up, partly by the leaves, but chiefly by the roots, are decomposed in the leaves; the oxygen is liberated, whilst the carbon and hydrogen, with the hydrogen and nitrogen from ammonia, together with sulphur and phosphorus, combine to form the proximate constituents necessary for the food and fuel, which nourish animals, and support their respiratory and other vital processes.

We have just seen that the skin is the seat of a feeble respiratory process, consisting of an interchange of oxygen and carbonic acid. A small amount of oxygen may also be absorbed, and of carbonic gas exhaled, at the mucous surfaces of the stomach and intestines; for atmospheric air is swallowed, mixed with the saliva and food, and dissolved in the drink. But in animals generally, excepting in the very lowest, special *respiratory organs*, often consisting of a very complicated apparatus, are present.

The respiration of animals is performed, sometimes in air and sometimes in water, the former being termed *aërial*, and the latter *aquatic, respiration*. The Mammalia, including Man, all Birds, Reptiles, and Amphibia, amongst the Vertebrata, the Pulmo-gasteropods belonging to the Mollusca, and the Insecta, Arachnida, and Myriapoda amongst the Annulosa, are *aërial breathers*, and are provided either with complex hollow organs named *lungs*, with simpler *air sacs*, or else with

minute air-tubes, or *tracheæ*, all these organs communicating directly with the *atmosphere*. A certain number of the Amphibia, all the Fishes, the Mollusca generally, except the pulmonated Gasteropods, all the Molluscoida, the Crustacea amongst the Annulosa, and all the Annuloida, Cœlenterata, and Protozoa are *aquatic breathers*, and are provided either with projecting organs named *branchiæ* or *gills*, sometimes external, but more commonly concealed, or with internal *ciliated sacs* or *canals*, or with external *ciliated processes*, *discs*, or *surfaces*, always in contact with *water*.

In aërial respiration, the source of the oxygen taken into the body, is the atmosphere, into which the carbonic acid is given off. In aquatic respiration, although the breathing is subaqueous, so that the oxygen is taken up from, and the carbonic acid given off into, the water, still the ultimate source of the oxygen, is the atmospheric air dissolved in that medium. The solvent power of water for air, is very great, and owing to the greater solubility of oxygen than of nitrogen in water, the air held in solution in this fluid, contains an unusual proportion of oxygen.

The great importance of the function of respiration to animal life, is shown by the fact that its interruption, by mechanical or chemical interference with the respiratory organs, is speedily followed by death. Air-breathing animals are quickly suffocated by strangulation, by immersion in water, by placing them under the receiver of an air-pump and then exhausting it, by giving them only a limited supply of air, or by making them breathe gases not containing free oxygen. Aquatic breathers are as quickly destroyed, if the fluid by which they are surrounded, has been deprived of air by boiling, or by placing it under the receiver of an air-pump, and then exhausting it.

In studying the respiration of Man, and the Mammalia generally, we have to consider the structure of the organs of respiration, *i.e.* of the thorax and its muscles, the air-passages, and the lungs; the mechanism of respiration, or the respiratory movements by which air is alternately drawn into, and expelled from, the body; the movement of the air in respiration, and the capacity of the lungs; the changes which the air undergoes during respiration; the changes produced by this process upon the blood and the tissues; the circumstances which modify the respiratory interchanges, including the phenomena of asphyxia, and the effects of breathing bad air; and lastly, the

organs and functions of respiration in animals. Afterwards it will be necessary to consider the phenomena of Animal Heat, Light, and Electricity; and to discuss, in a separate Section, the interesting questions relating to the Dynamics of the Animal Economy.

THE ORGANS OF RESPIRATION.

The Thorax.

The *thorax* (vol. i. p. 27; figs. 10, 13, 14) is an osseocartilaginous framework filled in with soft tissues, which contains and protects the central organs of respiration and circulation. It corresponds with the dorsal region of the spine. In front, it is formed by the sternum and the cartilages and anterior parts of the ribs; behind, by the dorsal vertebræ and posterior portions of the ribs; and, at the sides, by the remainder of the ribs. Between these solid parts, are the intercostal muscles, which are overlaid, in parts, by other muscles.

The cavity of the thorax is conical, being narrow above and broad below. Its upper opening, enclosed between the first dorsal vertebra, the first ribs, and the top of the sternum, is wider transversely than from front to back; its plane inclines downwards and forwards. The lower opening, bounded by the ensiform cartilage, the last dorsal vertebra, and the lower ribs or their cartilages, is much larger than the upper one. It is also wider from side to side than from front to back, but its plane inclines downwards and backwards, so that the thoracic cavity is much deeper behind than in front.

The upper opening transmits—besides certain muscles of the neck, the large bloodvessels of the head and upper limbs, numerous nerves and lymphatics, the thoracic duct, and the œsophagus—the principal air-tube, the *trachea*, or windpipe, which leads to the lungs; the summits of the two lungs, ascend beyond this opening. The lower opening is closed by the musculo-tendinous, movable structure, named the *diaphragm*, which is itself arched, and reaches higher up on the right side; this opening transmits the œsophagus, the great vessels, the thoracic duct, and the vagi and certain sympathetic nerves.

The Air Passages.

The nose, pharynx, and larynx have already been described. The *trachea*, or windpipe, placed in the middle line, descends

from the larynx, on a level with the fifth cervical vertebra, to opposite the third dorsal vertebra, where it divides into two smaller air-tubes, named the *bronchi*, one for each lung. The trachea (fig. 110, 1) is about $4\frac{1}{2}$ inches in length, and from $\frac{3}{4}$ to 1 inch in width; it is wider in the male than in the female. Its anterior surface and sides are convex; its posterior surface is flattened. It is overlapped at its upper part, in front and at the sides, by the isthmus and lobes of the thyroid body; it

Fig. 110.

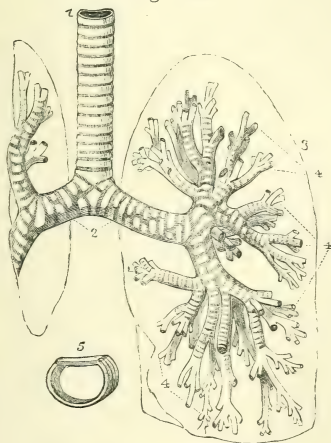


Fig. 110. Air-tubes of the human lungs, dissected out, and seen from the front. 1, trachea or windpipe. 2, the right and left bronchi, the right being the wider, the left the longer of the two. 3, outline of the left lung collapsed. 4, bronchia, or bronchial tubes in the lung, cut short. 5, transverse section of a portion of the trachea, showing the incomplete C-shaped rings, with the flat membranous part behind.

is also covered by certain muscles and vessels of the neck, and is concealed, lower down, by the upper part of the sternum and by the remains of the thymus gland. In the thorax, the large bloodvessels are in front of it, but in the neck, it is placed between them. Behind, its flattened surface rests on the œsophagus, by which it is separated from the spinal column. Its lower thoracic portion is placed in the space known as the posterior mediastinum, situated between the lungs.

The trachea is composed of from sixteen to twenty independent, transverse, incomplete hoops or rings of cartilage, held together by an intermediate fibrous coat, within which are muscular and elastic fibres and a mucous lining membrane.

The cartilages are flattened bands, incomplete behind, each being shaped like the letter C (fig. 110, 5), with its open part turned backwards. The first cartilage, which is suspended to the cricoid cartilage of the larynx, is the broadest; the last cartilage is V-shaped. The fibrous coat not only connects the cartilages together, but covers both their outer and inner surfaces; behind, where the cartilages are absent, this membrane is continuous. An external layer of longitudinal unstriped muscular fibres, is found connected with the fibrous membrane and with the cartilages; whilst an inner transverse set extends between the ends of the cartilages. Bundles of elastic fibres are placed immediately beneath the mucous membrane; at the posterior flat membranous part of the tube, they are seen as yellow longitudinal bands. The mucous membrane, continuous with that of the larynx and bronchi, has a columnar ciliated epithelium. Numerous tracheal mucous glands are found embedded in the walls of the tube, especially at its back part. Its nerves are derived from the pneumo-gastrics and the sympathetic.

The *right bronchus* measures about 1 inch in length; it is wider, and has a more horizontal direction, than the left bronchus; it enters the root of the right lung, opposite the fourth dorsal vertebra. The *left bronchus* is about twice as long as the right one; it is, however, narrower, and passes obliquely downward beneath the arch of the aorta, and in front of the œsophagus, thoracic duct and descending aorta, to enter the root of the left lung, opposite the fifth dorsal vertebra.

The structure of the bronchi is similar to that of the trachea; in front and at the sides, they are convex, and strengthened with incomplete hoops of cartilage, but behind, they are flat, membranous, and muscular. The cartilages are narrower and shorter than those of the trachea; in the right bronchus, there are from six to eight, and in the left, from nine to twelve.

The Lungs.

The lungs, fig. 13, *l, l*, are two in number, and occupy, *completely and accurately*, the lateral or pleural chambers of the thorax, one on each side of the pericardium and heart, *h*. Each

lung is free in all directions, except at a part of its inner surface, which is connected, by means of the bronchi and the pulmonary arteries and veins, with the trachea and the heart, fig. 111.

The lungs are porous, spongy organs, the tissue of which is so elastic, that, although they fill the closed pleural chambers, they collapse more or less, when the thorax is laid open. If squeezed, they give rise to a peculiar sensation called *crepitation*, owing to the air which is contained in them. Their size and weight present great variations, depending on their state of inflation, and the quantity of blood in their vessels, or of serum in their tissue. The average weight of the two lungs together, is, however, about 42 ounces, the right lung being about 2 ounces heavier than the left; they are larger in the male than in the female; they are moreover heavier, their proportion to the body being as 1 to 37 in the former, and as 1 to 43 in the latter. Owing to the air in the lungs, they float entirely, or even in portions, in water; the specific gravity of their substance, ranges from 345 to 746, water being 1,000. The colour of the lungs, varies at different periods of life; in the newly born infant, they are of a pinkish white; in the adult, they are darker, and become mottled with deep slate-coloured spots, patches, or lines, which increase in number and assume a deeper hue, as life advances, becoming, in some individuals, even black.

The surface of each lung, is invested by a thin, smooth, transparent, elastic serous membrane, named the *pleura*, which passes into certain fissures upon the surface of the lungs; at the root of the lungs, it is reflected upon the inner surface of the corresponding *pleural chamber* of the thorax, the whole of which it lines, forming a closed sac (see vol. i. p. 27). The parietal portion of this membrane, partly lines the sides of the thorax, where it forms the *costal pleura*; but, in the middle line, it covers a portion of the pericardium and other parts, and touches the opposite pleura; above, it closes in the upper opening of the thorax, reaching higher than the first rib; below, it lines the diaphragm. A triangular duplicature, forming the broad ligament of the lung, passes down from the root of the lung to the diaphragm, and serves to retain the lower portion of the lung in position. The free and moist surfaces of the parietal and pulmonary portions of the pleura, touch each other. If serous fluid, blood, pus, or air should collect between them, the *cavity* of the pleura becomes evident, and the diseases

known as hydrothorax, hæmothorax, empyema, or pneumothorax are developed. The right and left pleuræ are quite distinct from each other. The place where they come into contact, is just above the middle of the sternum; here they are connected together by areolar tissue, but in other parts of the middle line, they are separated from each other by an interval, called the *mediastinum*, in which all the parts contained in the thorax, except the lungs, are lodged. The right pleural chamber is shorter and wider than the left.

Each lung, as well as the pleural chamber into which it accurately fits, is of a conical shape, and presents an apex, a base, an outer and inner surface, and an anterior and posterior border. The *apex* is blunt, and projects into the neck, from an inch to nearly an inch and a half above the first rib. The *base* is broad and concave, and rests on the convexity of the diaphragm; its margin is thin, and passes between that muscle and the wall of the chest; it reaches much lower down at the outer side and behind than it does in front. The *outer surface*, smooth and convex, is in contact with the walls of the thorax, and is of greater depth behind, than in front. The *inner surface* is concave, being adapted to the pericardium and heart, behind which it presents a depression, called the *hilus*, where the bronchi and pulmonary vessels forming the root of the lung, pass in and out. The *anterior borders* of the lungs are thin, and partly overlap the pericardium, that of the right lung reaching to the middle of the whole length of the sternum, that of the left lung doing so only as low as the fourth costal cartilage. Above this point, the anterior borders of the two lungs, are merely separated from each other by their pleural membranes; but below it, the anterior border of the left lung forms, over the pericardium and apex of the heart, a V-shaped *notch*, the base of which is turned to the middle line (fig. 13). The *posterior border* of each lung, much longer than the anterior, is broad and rounded, and occupies the deep groove on either side of the vertebral column, reaching below, between the ribs and the diaphragm.

Each lung is divided, by a deep fissure, into an *upper* and *lower lobe*. This principal *fissure* extends from the posterior border of the lung near the apex, obliquely downwards and forwards, to the anterior border near the base. The upper lobe, on each side, is smaller than the lower one, and resembles a cone having an oblique base; the lower lobe has a somewhat quadrilateral shape. The upper lobe of the right lung,

is subdivided by a second fissure, which, passing forwards and upwards from the oblique fissure to the anterior border, cuts off a smaller triangular lobe, named the *middle* or *third* lobe of that lung. A rudimentary third lobe is sometimes present in the left lung. In the right lung, there are sometimes four lobes. The right lung is about an inch shorter than the left, and the concavity of its base is more pronounced; this corresponds with the higher position, and greater convexity of the right half of the diaphragm, over the right lobe of the liver. The right lung is also wider than the left, the breadth of the latter being diminished by the projection of the heart into the left half of the thorax.

The root of each lung, which is found on the inner surface somewhat above the middle, and much nearer the posterior than the anterior border, contains, as already stated, the bronchus, the pulmonary artery, and the two pulmonary veins; it also includes the nutrient vessels or bronchial arteries and veins, lymphatics and lymphatic glands, nerves, and areolar tissue, all being surrounded by a tubular reflection of the pleura. In the root of the lung, the pulmonary artery is placed behind the pulmonary veins, but in front of the bronchus, bronchial vessels, and lymphatic glands. The relative position of the bronchus and artery from above downwards, differs on the two sides; on the right side, the bronchus lies above the artery; but on the left side, the bronchus (fig. 111, 4), descending lower, to pass beneath the aortic arch, is placed below the artery, 6. The pulmonary veins, 7, 8, on both sides, are situated below the other structures.

The air tube, bloodvessels, lymphatics, and nerves found in the root of the lung, enter it, and, dividing and subdividing, penetrate not only its lobes, but reach certain much smaller portions of the lung substance, named the *lobules*. These lobules, which constitute the proper *pulmonary substance*, or *parenchyma*, are small compressed masses, which might be regarded as little independent lungs, or *lunglets*; they fit accurately against each other; they vary in shape and size, being, on the surface of the organ, large and pyramidal, with their base directed outwards, whilst in the interior, they are small and of irregular polyhedral shape. Each lobule is composed of a terminal branch of an air-tube, surrounded by a cluster of air-cells communicating with it; also of pulmonary and bronchial vessels, lymphatics, and nerves, with a fine interstitial areolar tissue. The lobules are supported on the terminal air-tubes, as if on

stalks, but they are likewise held together by the vessels, and by an *interlobular* areolar tissue, which attaches their sides together, and is itself connected with a general covering of areolar tissue, found upon the surface of the lung, beneath the pleura, named the *subpleural* or *subserous* coat. Both the interlobular and subserous tissues, contain many elastic fibres.

Fig. 111.

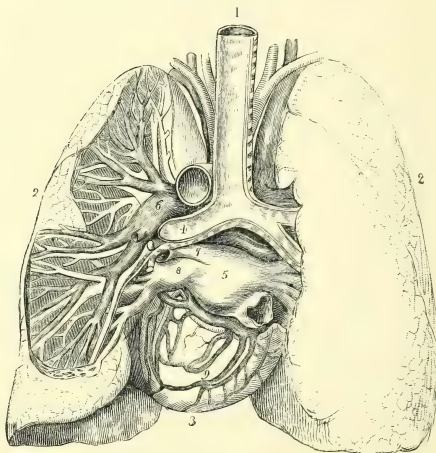


Fig. 111. Back view of the lungs and heart, with the air-tubes and great bloodvessels attached. 1, trachea or windpipe. 2, 2, lungs; the left one partly dissected, to show the bronchial tubes and the pulmonary arteries and veins branching in it. 3, heart. 4, left bronchus, entering at the root of the lung, beneath the arch of the aorta, which is seen cut across. 6, left pulmonary artery. 7, 8, left pulmonary veins, entering, 5, the left auricle; beneath the right pulmonary veins, is the inferior vena cava, cut across. 9, back or under surface of the left ventricle of the heart.

On entering the lung, each bronchus divides into an upper and lower branch, one for each lobe; but, on the right side, the lower branch gives off a smaller one, which passes into the middle or third lobe of that lung. Inside the lung, the bronchi continue to subdivide, at obtuse angles, into smaller and smaller tubes, called *bronchia*; these never coalesce again, but continue separate, after the manner of the primary ducts of a

gland, or of the branches of a tree. These tubes generally divide dichotomously, or in twos, but sometimes three bronchia proceed from a common trunk, or small lateral bronchia are given off. The finest bronchia, forming the *lobular bronchial tubes*, end in the lobules, as will presently be described. The combined sectional area of the smaller bronchia, is very much greater than that of the larger bronchia or the trachea.

Within the lung, the bronchia are round, and not flattened posteriorly, like the trachea and its primary divisions in the root of the lung. Their constituent elements are similar to those of the trachea, but these are here much modified. Thus, the cartilages, instead of being arranged in regular transverse slips, assume the form of angular or polygonal plates of proportionate size, placed on all sides of the tubes. At the angles of bifurcation of the tubes, spur-shaped pieces of cartilage usually support them; minute flakes are found even in the smaller bronchia. But the cartilages are absent in bronchia, the diameter of which is less than a quarter of a line; the walls of such tubes are entirely membranous. A fibrous coat and longitudinal elastic fibres, are present in all the tubes, down to the very smallest. The muscular fibres, of the unstriped kind, are no longer limited to the posterior portion of the tube, but, arranged in circular bundles, form a layer external to the cartilages; they extend to the smallest ramifications of the bronchia. The mucous membrane lining the bronchia, is thinner than that of the bronchi and trachea, with which it is continuous; it is covered with a ciliated columnar epithelium. The walls of the bronchi and larger bronchia, are provided with mucous glands.

The terminal bronchial offsets distributed to the lobules, or the *lobular bronchial tubes*, divide within the lobules, from four to nine times, according to the size of the lobule. The branches thus formed, become gradually smaller, being at length reduced to $\frac{1}{30}$ th, $\frac{1}{50}$ th, or $\frac{1}{70}$ th of an inch in diameter. They finally terminate in the so-called *intercellular passages*, or *air sacs*, which offer a marked contrast, both in form and structure, to the tubes; for instead of a cylindrical form, they appear like irregular passages, traversing the substance of the lobule at various angles, and communicating freely with each other; at the same time, they no longer present either longitudinal, elastic, or circular muscular fibres. Moreover, the diameter of the intercellular passages, is somewhat greater than that of the finest bronchial tubes from which they proceed,

and it increases a little at each division, whilst the tubes, in this respect, as already mentioned, diminish in size as they divide. Finally, the sides of the intercellular passages, at first smooth, like those of the lobular bronchial tubes, soon become recessed by numerous closely-set, sharply-defined, cup-shaped depressions; these are the so-called *air-vesicles* or *air-cells*. An intercellular passage may, indeed, be regarded as a space between the air-cells, which surround it on all sides.

Fig. 112.

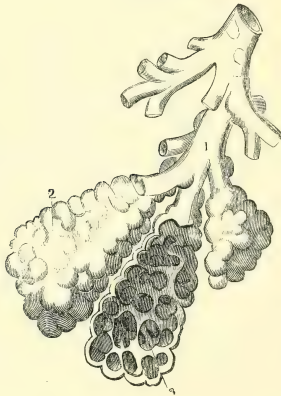


Fig. 112. Magnified diagrammatic view of groups or clusters of air-cells, one being laid open. 1, small bronchial tube, dividing into others which are membranous. 2, vesicular portion of lobule, with air-cells on its surface. 3, the same, laid open, to show the recesses or air-cells in its interior.

The *air-cells* or *air-vesicles* (fig. 112, 2, 3), the ultimate recesses to which the minutely subdivided air gains access, measure from $\frac{1}{200}$ th to $\frac{1}{70}$ th of an inch in diameter. They are smaller in the interior of the lungs, larger on the surface, and largest at the apices and thin edges of those organs. They are larger in the male than in the female, and gradually increase in size as life advances. Those cells which occupy the central portion of a lobule, appear like polyhedral alveoli, separated from each other by delicate septa. By some, it is

said that the sides of the cells are frequently perforated or deficient, so that neighbouring cells communicate with each other (Waters); but this is not universally admitted, at least as regards the human lung. The cells situated beneath the pleura, are four or six sided. No direct communication exists between the air-cells of adjacent lobules. The number of air cells in both lungs, has been calculated to be about 6,000,000. The walls of the air-cells, are thin and transparent, and are composed of areolar, mixed with fine elastic, tissue, lined by an exceedingly delicate mucous membrane, consisting of a thin transparent basement membrane, covered with a polygonal squamous non-ciliated epithelium.

The pulmonary arteries and veins are the functional, or respiratory, vessels of the lungs. The *pulmonary arteries*,

Fig. 113.



Fig. 113. Small portion of the inner surface of the air-cells, with the capillary network injected; the pulmonary capillaries are seen to be wider than the meshes between them.

unlike the systemic arteries, convey *venous* blood from the right ventricle of the heart to the lungs. The trunk of the pulmonary artery, having passed obliquely upwards and to the left, for about 2 inches, reaches the concavity of the aortic arch, and there divides into the right and left pulmonary arteries; each of these enters the corresponding lung, and divides into as many primary branches as there are lobes; these branches rapidly subdivide in company with the bronchia, and finally end in the *pulmonary capillaries*. These last-named vessels, placed beneath the mucous membrane of the air-cells and intercellular passages, form a delicate and close network composed of a single layer of small vessels, having exceedingly thin walls; their width varies from $\frac{1}{2400}$ th to $\frac{1}{4000}$ th of an inch; that of the meshes between them, is much less; at the

sides of adjoining cells, the capillary network is placed between their adjacent walls, so that it is acted on by the air on both sides. The venules which arise from the capillary network, quickly join to form larger trunks, which generally pursue a different route to that of the arteries; they finally end in *four pulmonary veins*, two from each lung, which convey the *arterialised* blood to the left auricle of the heart. The pulmonary veins are destitute of valves; their capacity is said to be about equal to, or even less than, that of the pulmonary arteries. Within the lungs the pulmonary arteries are usually situated above the bronchial tubes, and the pulmonary veins below. The *bronchial* arteries are the nutritive vessels of the lung; they are given off from the aorta, or from an intercostal artery, and are distributed to the walls of the bronchia and pulmonary vessels, to the interlobular areolar tissue and other neighbouring parts; they usually end in the bronchial veins, but the branches which supply the smallest bronchia end in the pulmonary capillary network. The *lymphatics* are superficial and deep, and terminate in the bronchial glands at the root of the lung. The nerves are derived from the vagus and sympathetic; connected with the latter, are numerous minute ganglia (Remak).

Mechanism of Respiration.

The respiratory movements are of two kinds—viz. those which draw air into the breathing organs, or the movements of *inspiration*, and those which expel the air from those organs, or the movements of *expiration*. A complete respiration therefore consists of an *inspiratory* and an *expiratory* act. Inspiration requires a greater effort than expiration. At the commencement of the independent existence of air-breathing animals, the former act precedes the latter, the lungs being then filled, before air can be expired from them; on the other hand, the final respiratory act consists of an expiration, and to expire is synonymous with to die.

Inspiration.—The thorax is a closed cavity, with movable walls, the available space in which, beyond that occupied by the heart and bloodvessels, œsophagus, thoracic duct, lymphatic glands and nerves, is accurately filled by the two lungs. The interior of these spongy organs, however, communicates with the outward atmosphere through the nose, mouth, pharynx, larynx, trachea, bronchi, and bronchial tubes. Hence any enlargement of the thoracic cavity, from expansion

of its walls, is immediately accompanied by the entrance of air, through the air-passages just mentioned, into the interior of the lungs, and by the inflation of those elastic organs, as they follow the expanding walls of the chest. In describing the inspiratory act, it is sometimes said that a virtual *vacuum* is formed in the thorax, which the air fills, by entering through the only passages by which it can reach its interior. But the vacuum in question, is only threatened or impending, none being really formed. The equilibrium between the atmospheric pressure on the surface of the lungs, acting through the walls of the thorax, and that on their interior, operating through the open air-passages, being disturbed by the active expansion of the thoracic parietes through the agency of the inspiratory muscles, the air enters the air-passages simultaneously, in exact and instant correspondence with the amount of expansion, and the lungs as instantly become inflated, and follow the inner surface of the expanding thoracic walls.

In this inspiratory movement, the thorax is enlarged in each of its three dimensions: in depth from before backwards, in width from side to side, and in length or height from above downwards (see fig. 114). The enlargement in *depth*, from the spine to the sternum, is accomplished by the elevation of the ribs, which being movably articulated with the vertebral column behind, and continued on, by their cartilages, to the sternum in front, and having, moreover, an oblique direction from their posterior to near their anterior extremities, necessarily cause an elevation and projection forwards of the sternum, when they are slightly lifted upon their posterior points of attachment, to a less oblique position. The point of support or fulcrum of each rib, is the vertebral column; whilst the connection of the upper ten ribs in front, directly or indirectly, with the sternum, enables them to elevate and push forward that bone, and thus, to increase the antero-posterior diameter of the chest. The enlargement of the thorax in *width*, is likewise accomplished by the elevation of the curved and obliquely attached ribs; for by such a movement, as may be illustrated on the skeleton, or on an apparatus consisting of pieces of hoops attached obliquely to a common upright support, the ribs, in becoming more horizontal, are not merely lifted, but slightly rotated on their hinder attached extremities; their sides are thus carried outwards, their outer surfaces being turned somewhat upwards, and their inner surfaces downwards. The total result, as it affects all the ribs,

is to expand the thorax in its transverse diameter. Lastly, the increase in the vertical diameter or *height* of the thorax,

Fig. 114.

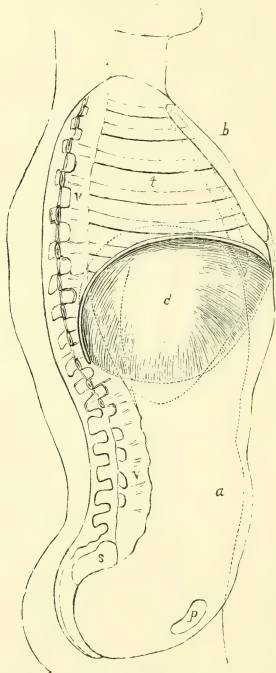


Fig. 114. Diagrammatic view of an antero-posterior section of the cavities of the thorax and abdomen, with the diaphragm intervening, to show the changes in the position of this septum, and of the walls of the chest and abdomen, in respiration; *a*, abdominal cavity; *t*, thorax; *v, v*, vertebral column; *d*, diaphragm. The dark lines show the position of the parts after inspiration, the dotted lines after expiration. *s*, section of the sacrum, and *p*, of the symphysis pubis, forming the posterior and anterior boundaries of the pelvic cavity, which communicates above with the abdomen.

which, in its costal portion, is diminished by the antero-posterior and transverse expansion, is accomplished by the

action of the arched or vaulted diaphragm, fig. 14, *d*, which forms the base of the thorax. The central tendinous expansion, the diaphragm, is drawn down by the contraction of its circumferential muscular parts; and this movement, named the *descent of the diaphragm*, causes an important elongation of the thoracic space.

Of these three modes of enlargement of the thoracic cavity, its elongation from above downwards, by the descent of the diaphragm, is by far the most considerable. In ordinary respiration, it constitutes in men, and, it is said, particularly in children, the principal respiratory movement; but it is accompanied by a slight lifting of the walls of the thorax, in front, at the sides, and especially at the lower part of the chest. When the diaphragm thus descends, the abdominal viscera do so likewise, and the abdominal walls, their muscles probably relaxing, become prominent; whilst in expiration, when, as may be supposed, the diaphragm ascends, the abdominal viscera are carried upwards, and the abdominal walls, slightly reacting, fall in. Hence, respiration performed, chiefly or entirely, by means of the diaphragm, is termed *abdominal*, *diaphragmatic*, or *inferior costal* respiration; it is the typical form of respiration in the male and in children. When breathing is mainly performed by the movements of the ribs, it is termed *pectoral* or *superior costal* respiration, and this is the characteristic form of breathing in the female, a fact which has been, by some, attributed to the habitual use of stays, but which may be a provision against the occasional impediment to abdominal respiration, which occurs in that sex. Over-distension of the abdomen, from any cause, as from gaseous or solid accumulations in the large intestine, tumours, or dropsical effusions, hinders abdominal respiration, the embarrassment to which is shown by the special efforts made to perform costal respiration. If the diaphragm contracted by itself, it would not only draw down its own tendinous vault, but would also pull the lower ribs downwards and backwards towards the vertebral column, and so diminish the lateral and antero-posterior dimensions of the lower part of the chest; but, in ordinary, and in deep inspiration, this tendency is counteracted by a proper adjustment of the force which raises the ribs.

The elevation of the ribs in inspiration, is accomplished, in ordinary breathing, by the cooperation of a number of small muscles placed deeply between, and upon the ribs. *First*, more especially concerned, are the *external intercostal* muscles. These

occupy the interspaces between all the ribs, extending, in each intercostal space, from close to the vertebral column to the neighbourhood of the costal cartilages; their fibres pass downwards and *forwards*, from one rib to another (see fig. 4). It was at one time supposed that these muscles, being placed between adjacent ribs, could not elevate those bones, unless the uppermost rib was first fixed, but that then each intercostal muscle could raise the rib below it. It has been shown, however, by observations on living animals, that the action of these muscles in elevating the ribs, does not require the previous fixing of the first rib. The mechanical principle on which this apparently singular result depends, may be illustrated by a simple apparatus, consisting of an upright support of wood, to which two bars are so attached at one end, by means of pins, as to be capable of being elevated or depressed; the bars themselves being held horizontally, a piece of vulcanised india-rubber is fixed tensely, and obliquely downwards and forwards from the upright support, between the bars—*i.e.* in the same direction as the fibres of the external intercostal muscles. When, now, the bars are drawn down, the india-rubber is stretched, and on being left free to act, immediately elevates both bars again, and supports them even in an oblique direction upwards. The explanation of this result is as follows:—the elastic force tends to approximate the *ends* of the piece of vulcanised india-rubber; this can only be accomplished by such a motion of the movable bars as will bring the *points*, to which the ends of the india-rubber are fixed, as near together, *i.e.* as nearly vertical to each other, as possible; and this results in the joint elevation of both bars. In the living body, the vertebral column represents the upright support, and the ribs the bars; but the effect is here modified by the somewhat fixed condition of the cartilages of the ribs to the sternum, which bone is, accordingly, moved upwards and forwards. *Secondly*, there are found at the back of the chest, near the spine, and descending from the several dorsal vertebræ to the subjacent ribs, muscles known as the long and short *levators of the ribs*. These not only assist in elevating the hinder parts of the ribs, but also slightly rotate them, so as to evert their lower borders. This slight rotation of the ribs, which accompanies their elevation, increases the diameter of the chest, and also widens each intercostal space along the sides of the thorax, where the ribs are more movable than at their anterior and posterior extremities. The elasticity of the costal cartilages, is highly

favourable to this elevation and rotation of the ribs, rendering both movements easier of execution, than if the costal framework were entirely composed of bone. *Thirdly*, besides the simpler action of the levators of the ribs, and the more complex movements of the external intercostals, it is certain that a portion of the so-called *internal intercostals* may, as will again be mentioned, also aid in elevating these bones and the sternum.

In deep inspiration, many more muscles come into play than in ordinary breathing. Thus, the anterior and posterior *scaleni* muscles, which descend, on each side, from the cervical vertebræ to the first and second ribs, aid powerfully in elevating those ribs, and, through them, perhaps all the others. The *posterior superior serrati* muscles, situated deeply, one on each side of the back of the chest, must also raise certain of the ribs. The *cervicales ascendentes* muscles will have a similar action. If the scapula, or shoulder bone, and the clavicle, or collar bone, are previously fixed by the muscles which descend to them from the head and neck, viz. by the *trapezius* (fig. 5, 2), *sterno-mastoid*, *levator* of the angle of the *scapula*, and greater and lesser *rhomboid* muscles on either side, then a very large and important muscle, the *great serratus* (fig. 4, 5), which passes from the base of each scapula, over the sides of the chest, to the eight upper ribs, must also assist powerfully in expanding the chest, by raising and drawing the ribs outwards. So, likewise, in front of the thorax, the *subclavius* muscle, which passes from the collar-bone to the first rib, and the *lesser pectoral* muscle, which descends from the scapula to the third, fourth, and fifth ribs, on each side, will then serve to elevate the ribs. In still more forced inspiration, when even the arms are fixed, by holding on to some external object of support, the *great pectoral* muscles in front (fig. 4, 2), and the *latissimi dorsi* behind (fig. 5, 3), both of which, besides other attachments, are connected, on the one hand, with the humerus, and, on the other, with certain of the ribs, may then cooperate in the elevation and outward rotation of these latter bones, and thus assist in inspiration. All the muscles just mentioned, are named *auxiliary muscles* of inspiration; but a few of them only, those first described, are ordinarily employed in deep inspiration. In very extreme cases, however, nearly every muscle of the body may assist in inspiration, by fixing certain parts, and thus affording more efficient points of action to the proper respiratory muscles.

The chief work performed in the act of inspiration, consists in overcoming the elastic resistance of the costal cartilages, and lifting the weight of the ribs. The lungs themselves are passive, or rather their elasticity has to be overcome. These organs, becoming inflated in every direction from their roots, as they follow the thoracic walls, are necessarily enlarged in all directions, antero-posteriorly, transversely, and vertically. The elastic fibres of the air-tubes, yield both in a longitudinal and a circular direction. The elastic walls of the air-cells, are extended generally; so also are the interlobular and subserous areolar tissue, and the pulmonary and costal pleuræ. To facilitate the ingress of air, the air-passages, from the nose and mouth down to the interior of the lungs, are supported either by bones or cartilages, as, for example, by the cartilaginous alæ of the nostrils, the bones of the nasal cavities, the cartilages of the larynx, the incomplete cartilaginous hoops of the trachea and primary bronchi, and lastly, by the less regular, but well-adapted plates of cartilage of the secondary bronchi and the bronchia. As especially fitted to maintain the perviousness of the bronchia, the cartilaginous spurs placed at the angles of bifurcation of those tubes, deserve particular mention. Through simple, membranous tubes, however firm, the free and instant entrance of the air necessary to proper inspiration, would have been impracticable; and, moreover, such tubes would have quickly collapsed during expiration. At the larynx, the narrow triangular glottis has musculo-membranous margins; but the state of this aperture, is regulated by the nervous system, which exercises a special control over it, and though it may be voluntarily or involuntarily closed, it is habitually open.

Mechanical obstructions in any part of the air-passages, by excluding the air, may prove fatal. The forcible closure of the mouth and nose for criminal purposes, the wilful filling of the fauces with a handkerchief or cloth, the compression of the windpipe, the accidental impaction of pieces of food or of some foreign body in the glottis, closure of this aperture from spasm, or from swelling of the surrounding mucous membrane, a condition known as œdema of the glottis, the lodgment of masses of food, too large to be swallowed, in the œsophagus, and, lastly, the introduction of fluid in any quantity, as in drowning, operate in this way.

When the thoracic walls are so injured, that an opening exists through them into the pleural chamber, their expansion

is no longer followed by the proper inflation of the lungs ; but the air passing in through the artificial opening, to supply the threatened vacuum, the lung is subjected to equal atmospheric pressure both on its pleural surface and within its air-passages and air-cells, and owing to the elasticity of its component structures, it collapses to a greater or less extent. If the opening be oblique or valved, as in certain punctured or gunshot wounds, some air may still enter the lung by the trachea. As the two pleuræ form distinct chambers, when one only is punctured, the corresponding lung alone becomes collapsed, and though respiration is embarrassed, death does not necessarily ensue. If, however, both pleuræ are simultaneously wounded, both lungs collapse, and death follows from asphyxia or suffocation.

Expiration.—The movement by which the air, having entered the lungs by an inspiratory effort, is again driven from them, is more passive in its character than that of inspiration, depending less upon muscular action, but more on the relaxation of the inspiratory muscles and on the elastic resilience of the organs and tissues concerned.

As the muscles of inspiration cease to act, the tendinous part of the diaphragm, the chief of those muscles, ascends into the thorax, followed by the abdominal viscera, which are supported in their upward movement by the cooperation of the muscles of the abdominal walls. At the same time, the ribs, and the sternum, which were elevated, descend, and fall back, whilst the effects of the rotation of the ribs, are counteracted by the elastic recoil of the costal cartilages. Lastly, the elasticity of the lungs themselves, plays a most important part, acting like an extended spring let loose, and serving to expel the air from the air-tubes and air-cells. The longitudinal and circular fibres of the bronchi and bronchia, shorten and narrow those tubes ; the elastic walls of the air-cells, diminish their size, and the interlobular, and especially the subpleural elastic tissues, aid powerfully in compressing every portion of the lung.

The importance of the elasticity of the component structures of the lungs, as an expiratory force, is shown by an experiment, which also illustrates the mode in which a lung expands by the removal of atmospheric pressure from its outer surface, and by the concurrent entrance of air, under its ordinary pressure, into the bronchial tubes. A bell-shaped glass jar, having a wide mouth below, and a strong open neck at its upper end, has the latter opening fitted with a perforated cork tightly

cemented in. The lower end of a glass-tube, about $\frac{1}{2}$ inch wide and 1 foot long, is closely secured into the bronchus of a sheep's lung; the upper end of this tube is then passed up into the bell-shaped glass jar, and pushed through the hole in the cork, until the lung is suspended high up in the jar; the tube is then hermetically cemented to the orifice in the cork, its upper end being left free and open. A piece of moistened bladder, in the centre of which a stop-cock is closely tied, so as to project outwards, is now placed loosely over the mouth of the jar, and is tightly secured to its rim, by cord. When the apparatus is held upright, the glass-tube represents the trachea, and the bell-shaped jar may be compared to the thorax, with this difference, however, that its sides are not movable, and are not in contact with the lung; lastly, the loosely extended moist sheet of bladder occupies the position of the diaphragm, the upward vaulted form of which may now be imitated, by opening the stop-cock in the centre of the bladder, thrusting this latter up into the bell-jar, and then closing the stop-cock. In this position, the bladder is supported by the atmospheric pressure, and the suspended lung is quiescent. On now pulling the stop-cock downwards, the bladder descends, imitating the descent of the diaphragm, the atmospheric pressure on the surface of the suspended lung is removed, and, in anticipation of the threatened vacuum, air enters through the glass tube into the interior of the lung, which, as may be seen through the jar, immediately becomes inflated. In this condition, the elastic tissues of the lung are put upon the stretch. But if the stop-cock be let go, the elastic resilience of this organ, causes the lung once more to contract, and the artificial diaphragm of moist bladder again ascends into the jar, until the atmospheric equilibrium inside and outside the lung, is re-established. The experiment may be repeated again and again, the accidental entrance of an excess of air between the sides of the jar and the surface of the lung, being remedied by opening the stop-cock, thrusting the bladder well up into the jar, and then closing it again. If desired, a manometer may be adapted, by a separate opening, to the top of the jar, so as to measure the expanding force used in distending the lung, as the bladder is drawn down. The two lungs of a dog, connected with the trachea, answer for this experiment as well as the sheep's lung; but the elasticity of the lung of the seal or the lion, is much greater. The elastic force of the human lung, has been calculated at 8 oz. per square inch of surface,

being equal to about 150 lbs. in the male, and about 124 lbs. in the female (Hutchinson).

It has been shown experimentally, that the contractility of the unstriped muscular fibres of the air-tubes, is excited by electricity, as well as by chemical and mechanical stimuli; and it has been suggested that they may assist in expelling air from the lungs; but the slow action of organic muscular fibres, renders it unlikely that they cooperate in movements so rapid as those of respiration; it is more probable that they regulate the diameter of the air-tubes, and perhaps aid in expelling mucus, or other secretions, from the smaller tubes. The cilia, which exist throughout the air-tubes, from the entrance of the air-cells upwards beyond the larynx, not only assist in the diffusion of moisture over the interior of these tubes, but perhaps also in retaining particles of dust which abound in the air, and so preventing their reaching the air-cells, and likewise in impelling upwards towards the glottis, mucus and entangled particles of matter. The current produced by these cilia, always sets in the upward direction.

Ordinary expiration is undoubtedly aided by certain proper expiratory muscles, especially by the *internal intercostals*. These muscles occupy only the anterior three-fourths of the intercostal spaces, being absent at the back part of the chest; they are placed inside the external intercostals. Their fibres pass, in each space, from above, downwards and *backwards*, or in the opposite direction to the fibres of the external intercostals. As already alluded to, the forepart of these muscles near the sternum, especially of the four or five upper ones, is said to assist in elevating the ribs in inspiration; but, elsewhere, these muscles depress the ribs, invert their lower edges, and diminish the width of the intercostal spaces, thus acting as expiratory muscles, diminishing the capacity of the thorax both from before backwards, and in width. Within the internal intercostals are situated the *infracostals*, small muscular bundles, having the same direction as the internal intercostals, but reaching over two or three spaces; they are also expiratory muscles. The *triangulares sterni*, small thin muscles, found on the internal surface of the sternum and cartilages of the true ribs, likewise cooperate in expiration; some maintain, however, that a portion of these muscles is inspiratory. The *auxiliary muscles of expiration*, are the upper part of the *serratus magnus*, when the scapula is previously fixed; the *posterior inferior serrati*, which pass from certain dorsal and

lumbar vertebræ upwards to the last four ribs; the *quadrati lumborum* muscles, which ascend from the pelvis and lumbar vertebræ to the lower ribs; certain portions of the long muscles of the back, known as the *erectores spinæ*; and, lastly, the abdominal muscles which are concerned in drawing the lower ribs downwards and inwards, such as the *external* and *internal obliqui*, the *transversales*, the *recti*, and *pyramidales* muscles. The abdominal muscles assist, even in ordinary expiration, by supporting or raising upwards and backwards the abdominal viscera, when the relaxation of the diaphragm causes these to ascend. In extremely forcible expiration, as in powerful inspiration, all the muscles of the body may be brought into some action. It is remarkable that a single small muscle, the *arytenoid* (vol. i. p. 258), which closes the aperture of the glottis, may, by an act of the will, be made to counteract the powerful efforts of the ordinary and auxiliary muscles of expiration. Under this condition, the walls of the thorax are rendered tense and firm, so as to form a solid base of support for the forcible use of the upper limbs. So also in voluntary or involuntary abdominal expulsive efforts, the chest is usually first filled by an inspiratory act, in which the diaphragm descends, and then, the glottis being closed, the diaphragm is fixed, and the abdominal and auxiliary expiratory muscles come into action, so as to compress the abdominal contents.

The movements of inspiration and expiration which constitute a complete respiratory act, succeed each other alternately, from the moment of birth until that of death; and this character of succession is named the *rhythm* of the respiratory acts.

The *number* of complete respirations in a given time, varies according to many conditions. In the adult, the respirations vary from 14 to 18 per minute; in childhood, at about five years of age, they are said to be about 26 per minute; whilst at birth, they are as many as 40 to 50; in extreme age, the frequency of the respirations is again increased. Persons of small stature, breathe more quickly, but less deeply, than taller people. The respirations are less frequent, but deeper in the male, than in the female. The number of respirations is increased by exercise and work, by food, stimulants, and moderate cold, and at great altitudes; whilst it is diminished in sleep, by moderate heat, by increased barometric pressure (see p. 220), by starvation, and by depressing influences and agents generally. It is curious that if the attention be

directed to the breathing, the number of respiratory acts is usually diminished. In quick walking, the respirations may be 30 in a minute; in running, 70; and in violent efforts, as many as 100 per minute. In sleep, the respirations are slow, because the interval between expiration and inspiration, is unusually prolonged. As elsewhere noticed, there is a certain ratio, in health, between the number of the respirations, and that of the beats of the heart, the proportion between them being in the adult, usually about 1 to 4. In childhood, the respirations are relatively quicker, their proportion to the pulse, being from 1 to 3 or $3\frac{1}{2}$. The ordinary ratio between the respirations and the pulse, is maintained in the daily and seasonal variations of the latter. But in certain diseases, it is seriously disturbed, and forms an important guide in medical practice; thus in pneumonia or inflammation of the lungs, the respirations are so quickened, through embarrassed function from congestion of the vessels, that the ratio may even be as 1 to 2. In hysteria, the respirations are also much increased in proportion to the pulse. In typhoid states, and in narcotic poisoning, the respirations become so slow, owing to some influence on the nervous centres, that their ratio to the pulse may be as 1 to 8.

The whole period occupied by a complete respiration, is divisible into three *stages*—viz. an inspiratory and an expiratory stage, followed by a *pause*, or stage of rest. According to some, there is also a pause between inspiration and expiration, but this can very seldom be recognised or measured. The total period of a respiration, being represented by 10, the inspiratory movement occupies 5 parts, the expiratory 4, and the recognisable pause between this and the succeeding respiratory act, 1. The period of motion, to that of rest, is therefore as 9 to 1 (Walshe). According to Vierordt, the period of inspiration being equal to 10, that of expiration, together with the pause, is, in deep respirations, 14; in quick breathings, 24. As he estimates the pause at one-fifth of the whole period, the numbers representing the inspiration, the expiration, and the pause, would, in the former case, be 10, 9, and 5, and in the latter 10, 17, and 7. According to recent observations with the sphygmograph and kymographion, the whole respiration period being 15, inspiration occupies 4, expiration 2, and the pause 9 parts; the ratio of the movement to the pause, is as 2 to 3 (Sanderson). In the disease

called emphysema, which consists in a dilatation of the air-cells, the periods of expiration and inspiration are equal, or the former is even longer than the latter. In cases of tubercular deposit, the expiration is also prolonged.

The force exercised by the inspiratory muscles in ordinary respiration, in an adult man, varies from about 1·5 inch to 4·5 inches of mercury; but, in exceptional cases, it may rise to even 7 inches. This force increases more rapidly than the actual amount of expansion of the chest, for when, in the same body, 70, 90, 190, and 200 cubic inches of air were injected into the lungs, the pressure was found to be 1', 1·5, 3·25, and 4·5 inches of mercury. The expiratory force is, on an average, about one-third or one-fourth stronger than the inspiratory force, varying from 2' to 5·8 inches of mercury, and rising even, in certain cases, to 10' inches (Hutchinson). This is due to the cooperation of the elasticity of the lungs, and the resilience of the chest walls, with the muscular effort. The force of the inspiration, is, therefore, the severer test of the strength of the body. The expiratory power is said to be greater in men of 5 feet 7 or 5 feet 8 inches in height, than in those either above or below that stature.

The entrance and escape of the air into, and out of, the air-tubes and air-cells, during inspiration and expiration, produce certain sounds named *respiratory murmurs*, which may be heard by the ear placed on the chest or by aid of the stethoscope. In health, the inspiratory and expiratory murmurs, named the bronchial or *tubular* sounds, which depend on the movement of the air through the air-tubes, are heard over the site of the larger bronchia, between the scapulæ, and over and near the upper part of the sternum. They are distinct and characterised by a soft blowing noise; those of inspiration and expiration, are of nearly equal duration. The *vesicular* respiratory murmurs, dependent upon the entrance and escape of the air in, and out of, the air-cells, are only faintly audible, like a gentle breezy noise; the expiratory vesicular murmur is weaker, and three or four times shorter, than the inspiratory murmur. The duration of the sounds, is altered by the same causes as those which modify the length of the movements of inspiration and expiration.

Accumulations of mucus or other secretions in the air-tubes, produce abnormal sounds, which are named *rhonchi*, or *râles*. These vary in character, according to the seat, quantity, and nature of the secreted matters. Thus, a fine *crepitant* rhonchus is produced by fluid exudation

in the air-cells, in pneumonia; a *sub-crepitant* rhonchus arises from the bubbling of air through fluid in the smaller air-tubes; a *sonorous* rhonchus, with its snoring, rasping, and cooing varieties, depends on obstructions in the larger air-tubes; a *sibilant*, or *whistling*, rhonchus is caused by mucous accumulations in the air-passages; and, lastly, a *cavernous* rhonchus is produced in cavities, or caverns, in the lung, formed in the destructive stage of phthisis. Peculiar, harsh, rubbing, or grating noises, named *friction sounds*, frequently heard in inflammation of the pleura, are caused by the rubbing of rough exudations of lymph effused on the pulmonary or costal pleura. Again, the relative amount of air and tissue in different parts of the thorax, causes differences in the sounds produced by *percussion* with the fingers, or otherwise, at different points of the thoracic surface. The percussion sound over the lungs, is more hollow, or, as it is termed, *resonant*, than over the heart, or great bloodvessels; the ascent of the convex liver into the concave base of the right lung, the two being of course separated by the diaphragm, alters the percussion sound, by diminishing the resonance at the base of the right side of the chest. The chest is more resonant over the great bronchi, than at other parts of the lungs. The resonance is everywhere greater in thin persons. Various changes in the lungs, produce great alterations in the resonance of the corresponding parts of the chest; congestions, thickenings, consolidations, accumulations of fluid as in hydro- or hæmo-thorax, or empyema, and the presence of tumours, cause dulness in the percussion sounds; whilst an abnormal amount of air, either in dilated or ruptured air-cells, as in emphysema, or in the cavities excavated in the lung-substance, as in phthisis, or in the pleural chamber, as in pneumo-thorax, cause an increased degree of resonance on percussion. Lastly, the term *vocal resonance* is applied to the sound heard on the surface of the chest, whilst the person is speaking; it is also modified by various internal conditions. A vibration felt on the walls of the chest, during speaking, is called the *vocal fremitus*.

The *rhythmic* movements of respiration, are governed by a special part of the nervous centres, cooperating with certain nerves. The rhythmic movements of the heart, not yet fully explained, are performed by a muscular organ, itself entirely uninfluenced by the will. But the muscles of respiration are truly subject to the will. We can increase or diminish the rapidity and force of these movements, according to our pleasure; we may imitate them, and can interrupt or arrest them at any chosen point of the respiratory act. This latter power is, however, of limited duration. Very prolonged interruption of the respiration, produces convulsions. But, even after a period of from twenty to thirty seconds, there arises, when the breath is held, a feeling so distressing, that it overcomes the most powerful volition. This feeling, termed *want of breath*, at last irresistibly compels the resumption of the respiratory acts. Like other sensations, it has its seat in some

portion of the grey substance of the nervous centres, and these being irritated, excite the motor nerves of the muscles of inspiration, which are then thrown into involuntary action. The ordinary respiratory movements are also involuntary; they continue to be regularly performed during the profoundest sleep, in a state of coma, in deformed infants in which the cerebrum is deficient, and, for a time, even in animals after the head has been removed.

The respiratory movements are, indeed, the most striking examples of reflex movements in the body. Their nature has already been generally discussed (vol. i. p. 346). The afferent or excitor nerves of inspiration are the pulmonary branches of the pneumo-gastric and sympathetic nerves, which latter contain fibres derived from the spinal cord; also the cutaneous nerves of the face belonging to the fifth cranial pair, and the cutaneous nerves of the body generally. The nasal nerves and the laryngeal branches of the pneumo-gastric, excite expiratory movements, as in sneezing and coughing. The nervous centre which governs the respiratory movements, is a limited portion of the grey matter of the medulla oblongata opposite the roots of the pneumo-gastric nerves, as has been proved experimentally (vol. i. p. 354-5). The so-called *vital knot*, at the back of the medulla, corresponds with the interval between the occipital bone and the arch of the axis; in this space, an animal may be suddenly killed by introducing a sharp, strong knife, so as to *pith* it, or divide the medulla. The efferent or motor respiratory nerves are: the phrenic nerves, which supply the diaphragm; the intercostal nerves, which supply, amongst others, the muscles of that name; the *long thoracic*, or so-called *external respiratory nerves* of Bell, which are distributed to the serrati muscles; the *spinal accessory* nerves, which supply the trapezii muscles; and the *facial* nerves. In extreme respiratory efforts, other motor nerves, are of course concerned. The reflected stimulus is conveyed to the roots of these nerves, along a particular tract of the spinal cord, situated behind the anterior roots of the spinal nerves, and descending along the lateral columns of the cord, from between the olivary and restiform bodies; this is the *respiratory tract* of Sir C. Bell, but, except as a path of special conduction, it has no respiratory influence. It is remarkable that the phrenic nerves which supply the diaphragm, the most active muscle in inspiration, arise from the cervical plexus, and therefore from a part of the cord much higher than the roots of the

highest intercostal nerves. Hence it happens that in certain injuries or diseases of the spinal cord, when the seat of these is above the origins of the intercostal, but below those of the phrenic nerves, costal respiration may be entirely abolished, whilst diaphragmatic breathing goes on. In such cases, however, death ultimately occurs from asphyxia, caused by the slow exudation of fluid into the lungs.

The respiratory movements being regarded as reflex or excito-motor, the first act of inspiration performed at birth, is said to be induced by the stimulus of cold acting on the excitable extremities of the fifth cranial nerves, which supply the nasal fossæ and the skin of the face, and also on those of the cutaneous nerves of the whole body. Cold, or a smart blow applied to the surface of the body of an apparently still-born infant, will sometimes excite inspiration; and, moreover, if the face of an infant be protected by warm covering, the first inspiratory act may be postponed (Marshall Hall). Once established, the reflex respiratory movements are believed to be excited by a peculiar stimulus, accompanying the sum of disagreeable sensations included in the feeling of want of breath. By some, it is supposed that the venous blood, deprived of oxygen, and loaded with carbonic acid gas and other effete matters, owing to the periodic interruption to the process of oxygenation, may be the cause of some of those disagreeable feelings, and may periodically stimulate the medulla and spinal cord, and so rhythmically excite the motor nerves of inspiration; according to others, it is rather the want of oxygen, which excites the movements, for an excess of that element enfeebles them.

The division of one vagus nerve in an animal, as a rule, lowers the frequency of, and embarrasses, the respiration, and the lungs become sometimes, but not always, the seat of extravasations of blood. Division of both vagi nerves in the neck, immediately diminishes the frequency of the respirations to one-half, and later to one-third, or even one-fourth, of the normal number; the inspirations become not only slower, but deeper, embarrassed, and puffing, or spasmodic; the expirations, on the other hand, are shorter; whilst the pause between the expiration and the succeeding inspiration, becomes more and more prolonged, which accounts for the diminished number of respiratory acts in a given time. Death usually takes place after from two to six days; the blood first becomes darker, as indicated by blueness of the lips, the tem-

perature sinks, and the animal dies of asphyxia. Congestion of the pulmonary vessels, extravasations of blood, and exudations of frothy sanguineous serum and mucus, are found in the air-cells and bronchial tubes, and partial solidification of the lung tissue occurs. Sometimes, however, death appears to ensue from disturbance of the digestive functions; but if these be recovered from, the animals may then live for many days. The continuance of the respiratory movements, for a time, after division of the pneumo-gastric nerves, depends on the excitability of the other afferent nerves of the body, especially of those of the skin. It seems doubtful whether the unstriped muscular fibres of the bronchial tubes, can be excited through the pneumo-gastric nerves. Their contractility is soon exhausted by stimuli directly applied to them; moreover, it is lessened by certain narcotics, especially by belladonna and stramonium; hence the use of such remedies in asthma, in relieving the paroxysms of dyspnœa, which are supposed to be due to a spasmodic contraction of these organic muscular fibres.

The respiratory apparatus is employed, either voluntarily or involuntarily, in many other acts necessary to the economy, or conducive to its comfort. In these, the movements of respiration are sometimes accelerated or strengthened, and sometimes diminished or checked.

Thus, *speaking, singing, shouting, and whistling*, are volitional movements, requiring special voluntary efforts of expiration, often modified and graduated in the most varied yet exact manner, and supported by inspirations performed at stated and suitable times. The act of *spitting* consists of a sudden expiration, accompanied by a peculiar position of the tongue, lips, teeth, and cheeks, having for its object the expulsion of saliva or other accumulations, from the mouth.

The semi-voluntary or involuntary acts which necessitate the cooperation of the respiratory apparatus, are much more varied. Thus, *coughing* is a sudden, strong expiration, accompanied by a peculiar noise, following a closure of the glottis and of the upper opening of the larynx, and usually preceded by a deep inspiration, to give effect to the cough. A column of air, suddenly driven from the air-tubes, as suddenly opens the glottis, and, being forced through the mouth, moves on accumulations or foreign bodies, and expels them from the bronchi, trachea, and larynx. *Sneezing* consists of a quick

noisy expiration, following a decided, sudden, and deep inspiration; but the glottis is not closed, as in coughing, and the column of air is not driven through the mouth, but is directed, by the closure of the fauces, into, and through, the nasal fossæ. The irritation which causes sneezing, has its seat in those fossæ, whilst that which induces coughing, as is well known, resides in the fauces, the larynx, especially at the glottis, or in the air-tubes. The stimuli which excite coughing, are cold air, irritating gases, fluids or solids, and diseased secretions. The noise of sneezing, is produced in the nose; whilst that of coughing, originates at the glottis. *Snoring* is produced by the resonance of the air passing, in or out, through the nasal cavities and the throat, owing to some irregular vibrations of the soft palate and uvula; it is sometimes dependent on narrowing of the fauces by enlargement of the tonsils, or on other peculiarities of conformation. In snoring, there is no special modification of the respiratory movements themselves, either as to force, frequency, or quickness. *Yawning* consists of a deep prolonged inspiration, the air being drawn in through the mouth, which is widely opened, by a consentaneous spasmodic action of the muscles of the lower jaw; this is then followed by a slow expiration, accompanied usually by a lifting of the soft palate, and sometimes by a prolonged characteristic sound. It may be accomplished by the will, and is often the result of involuntary imitation. *Sighing* also consists of a slow, deep inspiration, mostly accomplished through the mouth, and followed by a prolonged expiration, likewise associated with a peculiar sound; it often occurs after the attention has been strongly fixed; it is usually emotional. *Sobbing* is produced by rapid convulsive contractions of the diaphragm, associated with closure of the glottis. In *crying*, the movements resemble those of laughter, to be next described, although they are excited by very different emotions. *Laughing* consists of a series of sudden, short expirations, quickly succeeding each other, and divided, as it were, by intermediate closures of the glottis, giving rise to peculiar interrupted sounds. Laughter furnishes an excellent example of a reflex respiratory movement, excited either by sensori-motor impressions acting through certain cutaneous nerves, as when it is caused by tickling; or by emotional stimuli, as when it is the result of joy; or by a volitional stimulus, as when it is imitated by the actor. Lastly, *hiccup* is a short, sudden inspiration, produced by a sharp, convulsive contraction of the diaphragm, at the

end of which the glottis is suddenly and spasmodically closed, so that the air strikes it from below. Of these varied movements, some, such as sighing and yawning, may be induced by certain conditions of the respiratory organs themselves, whilst others, such as laughing and crying, are never so excited.

Movement of the Air in Respiration and Capacity of the Lungs.—After the lungs have been once inflated, as in the new-born infant, they are never, except from disease, entirely emptied of air. The most forcible expiration fails to accomplish this, and the quantity of air then retained in their tissue, is termed the *residual air*. The quantity, above this, held in the lungs after an ordinary expiration, but which may be expelled by a voluntary forced expiration, is called the *reserve air*, or sometimes the *supplemental air*. The quantity inspired and expired at each ordinary respiratory act, is called the *breathing* or *tidal air*; and the still further quantity, which can be drawn in by a forcible inspiration, is termed the *complemental air* (Julius Jeffreys). The total quantity which, after the deepest inspiration, can be expelled by the fullest expiration, is considered the measure of the so-called *vital capacity* of the chest or of the individual, because it shows the volume of air which is commanded by the vital movements of the thoracic walls. It is the extreme *differential capacity* of the chest, minus the space occupied by the residual air, which cannot be expelled; it represents the total difference between the fullest inspiration and the fullest expiration. This vital capacity in any individual, is of great importance, as indicating the extreme power of breathing in exercise or effort; and it furnishes highly significant information in certain diseases, especially in those of the lungs themselves (Hutchinson).

The determination of the actual quantities of air, which are the measures of the residual, reserve, breathing, and complemental air, and that of the total respiratory power or vital capacity of the chest, is extremely difficult. The elaborate and successful researches of Hutchinson, were made by means of his so-called *spirometer*. This apparatus is really a miniature gasometer; it consists of an inner cylinder, closed at its upper end, but open below, where it dips into water contained in an outer larger cylinder, which is closed below and open above; and it has a scale, by which its ascent and descent can be measured. The inner cylinder is accurately balanced, by weights attached to cords passing over pulleys affixed to the outer cylinder. The inner cylinder being depressed, and

allowed to fill with water, the person experimented on, blows air into it, by a tube which passes beneath its open mouth. The cylinder is raised, and when the expiratory effort is complete, the tube is closed by a stop-cock, so as to retain the air in the spirometer, and its quantity is read off upon the scale.

The *residual* air has been variously estimated at from 40 to 260 cubic inches; but, according to Hutchinson, it ranges from 75 to 100 cubic inches. It is most difficult to measure; for, after death, the lungs are not so empty of air, as they are after forced expiration during life, and it is not easy to estimate the difference. Besides, although the amount of residual air, corresponds generally with the size of the chest, it is influenced also by the relative mobility or stiffness of the walls, so that age, imparting rigidity to the costal cartilages, increases the residual, at the expense of the reserve or supplemental air. The residual and reserve air together, are taken, in the adult male, to be from 150 to 200 cubic inches (Hutchinson).

Accurate estimates of the so-called breathing air, and vital capacity, are of great importance. The *breathing air* has been differently calculated, from 10 to 92 cubic inches; but, according to the most recent observers, it ranges, in the adult male, from 16 to 20 cubic inches (Hutchinson), from 17 to 33 (Vierordt), from 16 to 25 (Coathupe), and from 30 to 39 cubic inches, in persons whose stature varies from 5 feet 7½ inches to 6 feet (Dr. E. Smith). A fair estimate for a person of mean height, 5 feet 6½ inches, would be about 20 cubic inches, for the average of the *day* and *night* respirations. The *vital capacity* in an adult male, of the stature of 5 feet 7 inches, is, on an average, about 230 cubic inches, the air being supposed to be at a temperature of 60°. The *complemental* air would therefore be 120 cubic inches.

The following are the estimated quantities, in cubic inches, calculated for the daily and nightly average, in a man of the stature of 5 feet 6½ inches:—

	Cubic Inches	
Residual Air	90	} Total displaceable Air, or Vital Capacity = 230 cubic inches.
Reserve Air	90	
Breathing Air	20	
Complemental Air	120	

Total Air after deepest Inspiration 320

These numbers cannot be regarded as absolutely accurate, but they illustrate the general proportions. The depth of an

ordinary inspiration, as measured by the breathing air, and the total displacement of air in forced respirations, indicating the vital capacity, differ much, according to the size of the body, but even in persons of the same age, height, and weight, they are liable to variation; for they do not merely depend on the size of the thorax, but necessarily on the *mobility* of its walls, and on the extent to which they are actually moved in the several inspiratory and expiratory acts. This may partly account for the great diversity in the estimates of the breathing air. The vital capacity has been shown to differ according to the *stature*; the variation in persons between the heights of 5 and 6 feet, follows a sort of law, every additional inch of height being accompanied by an average increase of 8 cubic inches in the vital capacity. Thus the capacity at 5 feet $6\frac{1}{2}$ inches being 230 cubic inches, that at 5 feet would be about 174, whilst that at 6 feet would be about 270 cubic inches. The vital capacity in women, is much smaller than in men, the proportion being almost as 1 to 2. It increases, in both sexes, from 15 to 35 years of age, at the rate of about 5 cubic inches per annum; whilst from 35 to 65, it diminishes by $1\frac{1}{2}$ cubic inch in a like period. The greatest capacity met with by Hutchinson, was in a giant 7 feet high, who weighed 308 lbs.; his capacity was 464 cubic inches. The minimum was 46 cubic inches, and occurred in a dwarf measuring 29 inches in height, and weighing only 40 lbs. Modern *dress* impedes respiration, for a man who could only expire 130 cubic inches when his clothes were on, accomplished 190 cubic inches when unclothed. The *posture* of the body modifies the vital capacity; for if, in the attitude of standing, it be 260 cubic inches, in the sitting posture it is 235, in the recumbent position 230, and in lying on the face 220. The degree of distension of the stomach, likewise influences the vital capacity of the chest. *Corpulency*, in persons weighing more than 160 lbs., diminishes the vital capacity, at the rate of 1 cubic inch for every additional pound up to 196 lbs. or 14 stone weight. *Practice* with the spirometer, increases the power of forcing up the inner cylinder, whilst nervousness and awkwardness operate the other way. Hence, in the use of this apparatus, allowance must be made for all the above-mentioned disturbing influences; and, it is certain, that the so-called vital capacity is not strictly related to the muscular power of the individual. Nevertheless, it is a valuable addition to our means of diagnosis, as to the condition of the lungs; the obstructed state of those organs in the

earlier stages of phthisis, and the deficient respiratory movement dependent upon this condition, cause a serious diminution in the vital capacity, as compared with the normal standard in persons of the same sex, age, and stature. A diminution of 16 per cent. in the normal capacity, is said to indicate a diseased condition (Hutchinson); but care must be taken to allow for the effects of congestion, and of abdominal disease.

If in a person 5 feet $6\frac{1}{2}$ inches in height, the breathing air averages, during the twenty-four hours of work, rest, and sleep, 20 cubic inches at each inspiration, and the number of respirations per minute for the day and night, be taken at 18, the quantity of air inspired and expired by an adult man of mean stature, in one minute would be 360 cubic inches. This would give 518,400 cubic inches or 300 cubic feet, for the twenty-four hours. This amount is less than the total daily quantity as estimated by Valentin, which is 688,348 cubic inches; less also than the quantity, viz. 686,000 cubic inches, found by Edward Smith to be the average in four adults, of a mean height of 5 feet $10\frac{1}{2}$ inches, during a state of rest. During ordinary exercise, the estimates of the last-named observer, give 804,780 cubic inches; in the case of the actively employed labourer, 1,568,390; and during a day's work, including twelve hours of Alpine exercise, 1,764,000 cubic inches. Vierordt's estimate for the twenty-four hours, is 732,000 cubic inches; but that author assumes the quantity of air inspired per minute, to be 450 cubic inches. Edward Smith found it to average 500 cubic inches in the day, and 400 during the night, in four persons of the mean stature of 5 feet $10\frac{1}{2}$ inches.

It has been estimated that, with a vital capacity of 200 cubic inches, the force employed in making the necessary full inspiration, is equal to the raising of 300 lbs. weight upon the surface of the chest; but in forcible expiration, the power exerted is much greater. In ordinary breathing, supposing the quantity of air inspired to be 20 cubic inches, the resistance overcome by the inspiratory muscles, is equal to a weight of 200 lbs.

Changes in the Air from Respiration.

The air expired from the chest, differs in three respects from that which is inspired. It is increased in *temperature*, except of course when the inspired air is already hotter than the body itself. It contains, as a rule, more *moisture*, unless

when it is previously, and exceptionally, saturated with watery vapour. Lastly, it undergoes important changes of *composition*, the chief of which consist in a loss of oxygen and an addition of carbonic acid.

The *increase of temperature* in the expired air, is regulated by the temperature of the air taken into the lungs. When the surrounding air is cold, the increase is not quite so great as when its temperature is nearer that of the body; but the difference is less than might be supposed. With the thermometer at from 50° to 68° , the expired air has a temperature of 95° to 100° ; whilst if the external temperature be 32° or freezing-point, then the expired air is not more than 86° . According to Valentin, however, in ordinary breathing, the temperature of the expired air in the winter, is only 1° less than that of the air expired in summer. In tranquil respiration, the expired air becomes comparatively warmer than in rapid breathing, as if, in the latter case, sufficient time was not allowed for the air to gain warmth. The increased warmth of the expired air, necessarily causes an increase of volume, but this is partly neutralised by a small loss of air in respiration, owing, as we shall see, to the absorption of more atmospheric oxygen by the lungs, than is equal to the carbonic acid exhaled. The actual volumes of the inspired and the expired air, are as 97.2 to 99.5; but, after the equalisation of their temperature, the volume of the expired air, is so reduced, that it becomes less, by the amount of oxygen absorbed in excess of that of the carbonic acid given out.

The *surplus of watery vapour* in the expired air, as compared with that in the inspired air, depending on the hygrometric condition of the air before it is breathed, it becomes difficult to estimate the daily quantity of water actually exhaled from the lungs. This has, however, been variously calculated at from 11 to 16 oz., or, as an approximate average, at 15 oz. per diem; but the quantity, according to modifying circumstances, ranges from 6 to 27 oz. The source of this vapour, is the water of the blood, and thus, like the aqueous basis of the secretions and excretions, it must assist in regulating the degree of fluidity of the blood. Some of the vapour of the breath, comes from the fauces, mouth, and nose, but the greater part, from the air-cells and air-tubes. It would seem that a small quantity of hydrogen is converted into water in the respiratory process, and may also come to be thus expelled. After taking food, or alcohol, the pulmonary exhalation is said

to be increased, but it is lessened during fasting. As a rule, the expired air is almost completely saturated with vapour, holding as much as it can dissolve, according to its temperature; but this is true only of calm respiration; for in hurried breathing, neither can the air be elevated to its highest temperature, nor can it be completely saturated with moisture. The more calmly air is breathed, the greater the loss of water by the lungs. Lastly, the *drier* the inspired air, the greater must be the amount of pulmonary exhalation; for, in breathing air already perfectly saturated, only such further quantity of water can be added to it, as its increase of temperature in the lungs, will enable it to dissolve. The inhalation of actual vapour, stops the pulmonary exhalation. So, too, when the temperature of the surrounding air, is 100° or 102° , and it is already saturated, the temperature of the blood itself being about the same, no further exhalation of water from the lungs, is possible; nor can the skin then give off more watery vapour. Under such circumstances, the kidneys, and perhaps also, though to a slight extent, the mucous membrane of the intestines, excrete more actively. The pulmonary exhalation contains, besides water, traces of carbonic acid, ammonia, chlorides, urates, and even some albuminoid substance, and it readily undergoes decomposition.

The changes in the *composition* of the expired air, are regulated by that of the inspired air. The composition of the atmosphere, in free space, is singularly uniform in different localities, and at different altitudes. By weight, supposing it to be dry, it contains nearly 77 parts of nitrogen, and 23 of oxygen. Besides these, its essential constituents, it contains a small percentage of carbonic acid, disengaged into it by terrestrial agencies, partly physical, such as volcanoes and springs, partly chemical, as the decomposition of carbonaceous matter, but chiefly organic, as from the respiration of plants; the atmosphere also presents minute traces of nitric acid, ammonia, and carburetted hydrogen, from the decomposition of animal and vegetable substances. In towns, it often contains sulphuretted hydrogen and sulphurous acid, from the combustion of coal; in the neighbourhood of chemical works, it may also be charged with chlorine, mineral acids and metallic substances. Under certain circumstances, a very pure air contains the important substance known as *ozone*, which is now usually regarded as a modification of oxygen. It is most abundant in sea air, in early morning, and, in England, with south-west

or west winds; it is almost absent with east winds, and is quite so in the centre of large towns, and in the atmosphere of dwellings.

By volume, dry air consists, in round numbers, of 80 volumes of nitrogen, and 20 of oxygen, or of 4 volumes of the former to 1 of the latter. A closer analysis gives, 79 volumes of nitrogen to 21 of oxygen. The quantity of carbonic acid gas averages .04 volumes per cent., or, as it is commonly expressed, 4 parts in 10,000.

The effect of a *single respiration* on the composition of the air breathed, is first, to remove from 100 volumes of air, about 5 volumes of oxygen, *i.e.* about $\frac{1}{4}$ th its normal quantity of that gas; and, secondly, to add to it, about 4 volumes per cent. of carbonic acid gas. Besides this, however, the quantity of nitrogen is slightly increased; and ammonia, carburetted hydrogen, certain salts, organic matter, and various undetermined volatile substances, are added to the air in the respiratory process.

The annexed Table, from Vierordt, shows the percentage composition, in volumes, of air, before, and after, it has been *once* breathed; the air being, in both cases, supposed to be perfectly dry. The minute trace of carbonic acid gas in unbreathed air, only .04 per cent., is here neglected.

	Atmospheric Air	Air once breathed
Nitrogen	79.2	79.3
Oxygen	20.8	15.4
Carbonic Acid	—	4.3
Loss	—	1
	<hr/> 100	<hr/> 100

During a single respiration, therefore, 5.4 parts of oxygen disappear, being absorbed by the lungs; whilst only 4.3 parts of carbonic acid are exhaled from those organs. Moreover, a minute quantity of nitrogen appears to be given off into the expired air. Lastly, owing to the excess of oxygen absorbed, over the carbonic acid exhaled, there is a loss of 1 per cent. of the air inspired. These results are founded on nearly 600 observations; but, as we shall hereafter see, individual experiments exhibit remarkable deviations, according to numerous circumstances.

Absorption of Oxygen.—The quantity of oxygen absorbed in respiration, is determined by careful examination of the quantity left in the expired air. This is done by using pyrogallic acid, which greedily attracts it, to take it up, or by com-

binning it with hydrogen, by means of the electric spark. There is no doubt that the greater portion of the oxygen absorbed, which in a single respiration is about $\frac{1}{4}$ th the total quantity in the air, combines somewhere, and in some way, with carbon, to form the carbonic acid which is exhaled. But as the carbonic acid produced, exactly equals in volume the oxygen concerned in its production, the surplus of oxygen absorbed over the carbonic acid exhaled, must remain in the system, and is probably therein combined with hydrogen, or with the sulphur and phosphorus of the albuminoid constituents of the body. In Man, from $\frac{1}{5}$ th to $\frac{1}{7}$ th of the total amount of oxygen absorbed, does not reappear in the carbonic acid, but remains to be combined with other oxidisable substances. In dogs fed upon carbohydrates, such as starch or sugar, or even upon milk, $\frac{9}{10}$ ths of the oxygen absorbed, are returned as carbonic acid, only $\frac{1}{10}$ th remaining in the system; if large quantities of flesh are eaten, more of the oxygen, *i.e.* $\frac{1}{3}$ th, is retained; lastly, when fat alone is consumed, $\frac{3}{10}$ ths are retained, as if a pure fat diet stimulated the oxidation of the nitrogenous tissues (Regnault and Reiset). Again, in Herbivorous animals, which consume many carbohydrates in their food, the proportion of oxygen retained in the system, is exceedingly small; whereas, in Carnivorous animals, the food of which is chiefly nitrogenous, but also fatty, a very large proportion is retained (Dulong and Despretz). In starving animals, also, which practically live carnivorously, *i.e.* on their own tissues, a large proportion of the oxygen is retained, amounting even to $\frac{2}{3}$ ths of the total quantity absorbed.

Elimination of Carbonic Acid.—The fact of the elimination of this gas from the lungs, may be shown by blowing slowly through a tube into lime water, which soon becomes turbid from the formation of carbonate of lime, more especially as the last quantities of air are being expelled from the chest. The determination of the quantity of carbonic acid gas given off in respiration, is extremely difficult, notwithstanding the ingenuity of the methods employed for this purpose.

The simplest method, used by Prout, Dumas, Vierordt, and others, consists in causing a person to inspire air through the nose, and expire it through a tube, held in the mouth, into a closed bag or receiver; and then in analysing the expired air, by agitation with lime-water or with a solution of caustic potash, either of these substances absorbing the carbonic acid, which can thus be measured. The oxygen has, at the same

time, been estimated, by means of pyrogallic acid, or by de-flagration with hydrogen, by means of the electric spark (Vierordt). Such a method, excellent for individual trials, is not adapted for general or comparative experiments; because the same person does not, under such conditions, breathe equally, at all times, even after considerable practice; nor can different persons breathe equally, in regard to each other, differences in the depth and duration of the respirations, rendering a comparison of the results fallacious.

For these reasons, observations have been made on men and animals, placed in suitable hermetically closed chambers, and able to breathe with less, or even no restraint. The *breathing-chamber* communicates with the air by means of a small supply tube on one side, and on the other, is connected, by a tube, with an *aspirator*, *i.e.* a second closed chamber filled with water; according as this water is permitted to flow from the aspirator, air is withdrawn from the breathing-chamber, whilst fresh air enters by the supply tube. To ensure the absence of carbonic acid from the air employed, the supply tube has a bend in it, containing a solution of caustic potash. The tube connecting the breathing-chamber with the aspirator, has also a bend containing asbestos, moistened with concentrated sulphuric acid, for the absorption of the exhaled water; besides this, it is fitted with a Liebig's potash-tube, for fixing and weighing the carbonic acid formed in respiration, and also with another bent tube, for again desiccating the remaining air. By such an apparatus, the quantity of air passing through the air-chamber, and the quantity of carbonic acid produced in any given time, can be determined (Dulong and Despretz's experiments on animals). In observations on men, the body has been enclosed in a second smaller box, so that the head alone projected into the air-chamber; the products of cutaneous respiration and exhalation, are thus separated from the pulmonary respiration and exhalation, the gases and vapour given off by the skin being retained in the smaller box, and those given off by the lungs being discharged into the breathing-chamber (Scharling's and Hannover's experiments on Man). By others, the face alone has been covered with a tight-fitting mask, through which a stream of air enters by two valved openings, and from which it is drawn off through a tube into a receiver, by means of an air-pump (Andral and Gavarret). Instead of supplying the breathing-chamber, in which animals have been placed, with pure atmospheric air,

known quantities of oxygen, proportioned to the quantity of carbonic acid formed, have been introduced. The arrangements necessary for the gradual absorption of the carbonic acid and the introduction of fresh oxygen, render this apparatus somewhat complex, but interesting results have been obtained by it (Regnault and Reiset). In long-continued experiments, however, the quantity of nitrogen in the chamber, gradually increases by exhalation from the animal's lungs; hence the atmosphere breathed by it, is no longer normal, and the respiration is modified accordingly.

The experiments of Pettenkofer and Voit, undertaken with the pecuniary assistance of the late King of Bavaria, are still more elaborate, costly, and complete. A large closed breathing-chamber is provided, in which the person experimented upon, can live and breathe for many hours as easily as in an ordinary apartment; and through it, copious streams of air, as much as 75 cubic mètres per hour, are drawn, by means of a double pump worked by a small steam-engine, the total quantity passed through, being accurately registered, after desiccation, by a gas-meter interposed between the chamber and the pump. Atmospheric air is admitted to the chamber by proper apertures, and the amount of carbonic acid gas and water already contained in it, is accurately determined. The contaminated air leaves the chamber by two tubes, one passing from near the ceiling, and the other from near the floor, which then join a common tube; this tube leads into a desiccating box, from which the dried air passes through the gas-meter to the cylinders of the double air-pump. To absorb and measure the whole of the carbonic acid gas contained in this large stream of air, the total product of the respiration of the person living in the chamber, would be an inconvenient process; accordingly, a small portion of the contaminated air is diverted for that purpose, through an analysing apparatus, into which this portion of the air is drawn by a peculiar suction- and pressure-pump, moved by the steam-engine which works the larger pump. This portion of air passes in succession, through an apparatus which absorbs and measures, first the water, and then the carbonic acid contained in it, and afterwards through a desiccating box and small gas-meter, by which it is ultimately measured. Its quantity, compared with the larger quantity drawn through the main tube, furnishes the means of calculating the total quantity of carbonic acid eliminated by the person confined in the breathing-chamber, in a given

time. The quantities of carbonic acid gas and water, formed by the combustion of a stearin candle in the chamber, may be determined by this apparatus, as correctly as by the ordinary process of organic analysis.

Dr. E. Smith has employed a small mask, which fits tightly over the mouth and nostrils, and is provided with a valved inlet and outlet. The air is inspired through, and measured by, a *spirometer* consisting of a delicate gas-meter. The expired air passes through a desiccator, containing sulphuric acid to absorb watery vapour; then through a gutta percha box, divided into many chambers and cells, containing caustic potash, and offering a surface of 700 square inches, so as to abstract the carbonic acid; and, lastly, through a second desiccator to retain any moisture carried off and lost, from the potash box. The increase in weight of the mask, with the connecting-tube and first desiccator, shows the amount of vapour exhaled from the lungs; whilst the addition to the joint weight of the potash box and the second desiccator, gives the weight of the carbonic acid expired.

Regnault and Reiset, Pettenkofer and Voit, and Dr. Edward Smith, have endeavoured to determine not merely the amount of carbonic acid eliminated, in ordinary breathing, but also the influence of those conditions which modify that amount, and likewise have attempted to obtain data for comparing the quantity of carbonic acid formed and of oxygen taken in, with the animal heat evolved.

Some only of the results obtained by various observers, can here be quoted. Dumas, calculating that by an adult male, of average size, 320 cubic inches of air are respired in one minute, and that this contains on expiration, 4 per cent. of carbonic acid, concluded that about 13 cubic inches of carbonic acid are exhaled per minute, which would be equal to a total of $5\frac{1}{2}$ oz. av. of carbon thrown off by the lungs in twenty-four hours. The calculations of Valentin and Brunner, Davy, Allen, Pepys, and Lavoisier, agree closely, yielding, as a general result, 8 oz. of carbon excreted by the lungs in twenty-four hours. Andral and Gavarret estimated the daily quantity at 9 oz.; Vierordt says that it varies from 5 to 8 oz. Dr. E. Smith found, as an average of eight experiments, the daily quantity, in a state of rest, in four men, whose mean height was 5 feet $9\frac{3}{4}$ inches, to be 7.144 oz.; the extremes were 5.6 oz. and 7.85 oz. With an ordinary amount of exercise,

he estimates the quantity at about $8\frac{1}{2}$ oz., and in a working man fully engaged in labour, at rather more than $11\frac{1}{2}$ oz.

Adopting as a basis of calculation, the estimate already given at p. 435, viz. of 300 cubic feet, or 518,400 cubic inches, as the total quantity of air respired in twenty-four hours, by an average-sized adult male, 5 feet $6\frac{1}{2}$ inches in height, allowing for the effects of work in the day and the influence of repose at night, and, moreover, calculating that the average quantity of carbonic acid in the air when expired is 4 per cent., then 20,736 cubic inches of carbonic acid would be given off in the twenty-four hours. As 100 cubic inches of carbonic acid gas, weigh 47.26 grains, this quantity would weigh about 9,800 grains, which would contain 2,672 grains, or rather more than 6 oz. av. of carbon. This is perhaps a fair calculation for a man of medium size, not engaged in any special exercise, or labour.

Elimination of Nitrogen.—The nitrogen of the atmosphere, which serves to dilute the oxygen, is, to a slight extent, absorbed by the blood, for that fluid always contains nitrogen in a state of solution. Nitrogen, however, is also given off from the blood through the breath; and the balance appears to be rather in favour of the process of elimination. The quantity thus thrown off by warm-blooded animals, is so minute as never to exceed $\frac{1}{50}$ th part of the oxygen consumed (Vierordt); sometimes it is less than $\frac{1}{100}$ th part (Regnault and Reiset). The source of this small excess in the nitrogen exhaled, was at one time supposed to be the nitrogenous aliments, the quantity of nitrogen excreted by the kidneys, skin, and intestines, being supposed to be less than that taken in the food. The quantity of nitrogen not accounted for in the renal, cutaneous, and intestinal excretions, has been said to be equal to $\frac{1}{15}$ th of the oxygen consumed in an adult, which nearly agrees with the estimate of Regnault and Reiset above mentioned. But, according to Voit and others, however, all the nitrogen of the food which is actually subjected to metamorphosis in the blood, is accounted for in the nitrogenous constituents of the urine. The minute and unimportant excess in the expired air, may, therefore, be derived from the atmospheric air, which is swallowed with the saliva, food, and drink, and is taken up by venous absorption; its oxygen being utilised in the blood, the nitrogen escapes through the walls of the pulmonary capillaries and the air-cells, into the breath. In favour

of this view, it may be added, that the decomposition of nitrogenous substances in the system, so as to yield free nitrogen, is unknown ; that in starving animals, which probably swallow less air, nitrogen is not given off in excess, but some of it seems rather to be absorbed ; and lastly, that whilst the quantities of oxygen and carbonic acid in arterial and venous blood, differ in a constant manner, the quantity of nitrogen follows no such rule, and even varies in both kinds of blood.

Other Substances Eliminated in the Breath.—Chloride of sodium, hydrochlorate of ammonia, uric acid, and urates of soda and ammonia, have been found in expired air. The carbonate of ammonia, frequently present, is sometimes partly derived from decaying animal matter between, or belonging to, the teeth ; but some of it is believed, by certain physiologists, to come from the blood. The carburetted hydrogen occasionally found in the breath, proceeds from the blood, into which it enters by absorption from the alimentary canal. The presence of organic matter in the breath, is detected by passing the expired air through strong sulphuric acid, which, in a prolonged experiment, becomes brown. According to recent enquiries, this organic substance is albuminoid, and when collected and allowed to putrefy, becomes extremely offensive ; when accumulated in small and over-crowded rooms, it has a fœtid, repugnant odour. It may possibly be the medium, or vehicle, of certain contagions thrown off by the breath ; it is not to be confounded with the bad smell from carious teeth, or from ulcers in the mouth, pharynx, or air-passages. Many odorous substances may exist in the breath, derived from food, drink, or medicines, such as cheese, alcohol, or perhaps aldehyde, given off after the use of alcoholic beverages, the volatile principles of garlic, onions, and spices, ethers, chloroform, camphor, musk, and many other medicinal substances. Phosphorus dissolved in oil, and injected into the veins of an animal, is given off by the lungs in some imperfectly oxidised state, so that the breath is luminous as it passes from the nostrils.

Effects of Respiration on the Blood and Tissues.

Changes in the Colour of the Blood.—The most obvious change effected in the blood, as it passes through the lungs, is that from the dark purple venous, to the bright scarlet arterial, tint. A similar change of colour takes place on agitating dark

venous blood with air, and, still more quickly, with oxygen ; it also occurs when venous blood is introduced into a moistened bladder, and suspended in air or in oxygen gas. The causes of this change of colour, have been the subject of much enquiry.

It is found that on adding water to bright arterial blood, it becomes of a dark hue ; whilst strong solutions of common salt, saltpetre, or bicarbonate of potash, when added to venous blood, immediately brighten its colour ; this effect has been attributed, either to the direct action of the saline substances, or else to the change which they produce in the specific gravity of the blood. It has been supposed that the red corpuscles, by exosmosis of fluid into the denser solution of the saline substance, shrink, and thus, from being slightly biconcave, become deeply so. On the other hand, the addition of water, has the effect of producing an endosmosis of fluid into the corpuscles, and so causes them to swell, and assume a flat or even biconvex form.

These opposite changes of shape have been supposed to modify the power of the corpuscles to absorb coloured light, more being absorbed when they are swollen, and less when they are shrunk. But, according to Professor Stokes, this explanation is inconsistent with optical principles, and the change of colour is due to a modification in the *refractive* power of the corpuscles ; in the shrunken state, their refractive power is increased, and, accordingly, a larger amount of reflection takes place from the surfaces of contact of the corpuscles with the surrounding fluid ; whilst in the distended state, their refractive power is diminished, and less reflection takes place from their surfaces. But, although the brilliant colour, produced by the addition of strong saline solutions to the blood, and the dark hue occasioned by diluting it with water, may be thus satisfactorily explained, the natural alterations of colour produced in the blood, by the respiratory changes, cannot be so accounted for ; though venous blood is of somewhat less specific gravity than arterial, yet there is no evidence of its containing fewer salts ; moreover, direct observation has failed to detect any difference in form, between the corpuscles of the two kinds of blood ; and lastly, the inadequacy of such a purely physical explanation, is proved by the fact that, even when the red corpuscles are entirely dissolved, or when pure solutions of cruorin or the colouring substance of the blood, are employed, precisely similar changes in colour ensue, from alternately agitating them with oxygen and carbonic

acid, in the former case, the colour being brightened, and in the latter rendered dark. The nature of the changes thus induced in the cruorin of the blood, has been revealed by the photo-chemical discoveries of Hoppe and Stokes, in which the so-called *spectrum analysis* is employed, to detect most recon-dite changes in the cruorin.

The formation of the prismatic *solar spectrum*, by passing a beam of sunlight through a prism, has already been explained (vol. i. p. 546). In this spectrum, when sufficiently magnified, it has long been observed, that numerous, fine, dark lines exist, the lines of Fraunhofer; these are owing partly to the presence of vapour in the air, which refracts some of the light, but chiefly to the absence, in the light examined, of luminous rays of certain degrees of refrangibility; the consequence of which is, that some parts of the spectrum are left unoccupied by any light whatever. In the solar spectrum, Fraunhofer described 80 *dark bands or lines*; but 2000 are now recognised. Light obtained from different sources, as by the combustion of different substances, or ordinary light first passed through transparent bodies, solutions, or even through the vapours of volatile substances, or proper gases, either *colourless* or *coloured*, and afterwards transmitted through a prism, also forms a spectrum; but on comparing the magnified spectra of different substances, it is found, in many of them, that the dark bands differ in number, position, width, and intensity; and, moreover, that in the case of certain lights, which are coloured, *colour bands* of different position, number, width, and intensity, make their appearance. The yellow colour band of sodium, is a remarkable example of this.

The *dark bands*, sometimes called *absorption bands*, and the *colour bands*, being characteristic and constant, for certain substances, they constitute most delicate means of detecting, and discriminating between, such substances. This is done by the *spectroscope*, an instrument consisting essentially of a tube with a slit at one end, a prism at the other, and a small magnifying glass with which to magnify the spectrum. This method is the so-called *spectrum analysis*, by which, not only have new substances been detected in chemical processes upon the earth, but some at least of the constituents of the luminous atmospheres of distant stars, have been determined. It has also been employed to follow the entrance of peculiar substances, such as lithium and cæsium, into the blood and tissues of living animals, to measure their rate of absorption, their preference for particular tissues, and their periods of excretion from the body (Bence Jones). To the same observer, we owe very interesting researches, in which the *fluorescent* property of quinine (vol. i. p. 547) is made use of, to follow that substance into, and out of, the living economy, by its presence or absence in the crystalline lens of the eye. It, moreover, appears that a peculiar animal substance, also fluorescent, and therefore named by Dr. Jones, *quinoidin*, is constantly present in the animal body.

Amongst other results of the spectrum analysis of coloured solutions, it was discovered by Hoppe, that dilute solutions of blood, produce *two* peculiar *dark* absorption bands of great beauty and distinctness, situated

in the spectrum, between the D and E lines of Fraunhofer, and having a remarkably bright *intermediate colour* band. He showed that this spectrum was formed by the coloured blood of animals generally; that the red colouring substance seemed to remain unchanged by the action of alkaline carbonates and caustic ammonia, for its spectrum remained unaltered; but that it was instantly decomposed by acids, and more slowly by caustic alkalies, a substance being then produced, which causes different absorption bands, and corresponds with the hæmatin of Lecanu.

This subject has since been further investigated by Professor Stokes. To examine the natural blood spectrum, he placed a small portion of blood well diluted with water, or a watery extract of the clot, in a test-tube; this being held up to the light, behind a fine slit in a piece of black card or a metal plate, and looked at through a prism, the two characteristic, sharply-defined, dark absorption bands, with the intermediate bright streak, were readily seen. On adding to the coloured solution, a reagent capable of *abstracting oxygen* from it, a remarkable change occurred in the spectrum. First, it became a little darker; but, besides this, instead of the *two* dark bands with their intermediate bright streak, a *single*, broader, and less defined band was now seen, situated nearly opposite the place of the bright band in the spectrum of the simple solution. Since the solution of blood is alkaline, and since acids, as just mentioned, decompose its colouring substance, it was necessary to employ a peculiar deoxygenating agent; the one selected, was a solution of protosulphate of iron, containing a small quantity of tartaric acid, which prevents the precipitation of the iron by alkalies; this was rendered slightly alkaline, by a little soda. On next exposing the deoxygenated and altered coloured solution to the air in a shallow vessel, or on agitating it with air, by shaking it in a long tube, it was found that the colour again became brighter, and that, on examination with the prism, the characteristic dark bands, with the intermediate bright one, again appeared. These changes were evidently attributable to the reoxygenation of the colouring substance by the oxygen of the air. This beautiful experiment realised the supposition previously entertained by Stokes, that he might imitate, and possibly explain, the change of colour of arterial into venous, and of venous into arterial, blood. That the single band of the altered solution, does not belong to the reagent, is shown by examining that separately; and that it is not produced by a compound of the reagent with the colouring substance, but simply by deoxygenation of the latter, is proved by the same effects being produced by other deoxidising agents, such as protochloride of tin, and hydrosulphuret of ammonia, and also by the ordinary and well-known displacement of oxygen, by means of carbonic acid. Moreover, these reagents have themselves no power to produce the newly-observed colour band.

From these experiments, it is concluded by Stokes, that there exists in the blood, a *natural colouring matter*, which might be named *cruorin*, capable, like the colouring matter of indigo, of assuming, by alternate abstraction and reintroduction of oxygen, two states of oxidation, in which it differs in colour

and in its action on the spectrum. The hæmatin of Lecanu is an artificial compound, produced by the decomposition of this cruorin by powerful acids, and is named by Stokes, *brown hæmatin*, to distinguish it from *red hæmatin*, formed by the oxidation of the brown variety, both of which show different absorption bands to those of cruorin.

The cruorin in its bright condition, is named *scarlet cruorin*, and in its dark condition, *purple cruorin*; the former gives the spectrum with two dark bands and an intermediate light one, and the latter, that with a single dark band. The purple cruorin, or deoxygenated kind, is supposed to exist in venous blood, and the scarlet, or oxygenated kind, in arterial blood. The evident attraction of cruorin for oxygen, is supposed to account for the absorption and combination of that gas with the blood; and thus also for the special attraction, or affinity, of the red corpuscles for oxygen, of which, indeed, they have been often named the *carriers*.

As apparently opposed to these conclusions, it is found that ordinary venous blood exhibits the spectrum of the scarlet cruorin, and not that of the purple cruorin; but this, as observed by Stokes, may merely show that most of the cruorin in venous blood, is still scarlet cruorin, the colouring substance being only partially converted into the purple condition. Venous blood, indeed, like arterial blood, still contains oxygen as well as carbonic acid, though in different proportions; and, although it is unequal to the perfect maintenance of the functions of the muscular and nervous substance, it is still better than no blood at all (Brown-Séquard). Moreover, extensive hemorrhage is not necessarily fatal; and persons affected with chlorosis, exhale carbonic acid as freely as those in health. It is possible, also, that carbonic acid may act less powerfully, when the blood is undiluted than when, as in experiments, it is mixed with water.

The cruorin of the blood being supposed, in the act of respiration, to undergo oxygenation as it assumes its scarlet colour, its deoxygenation, or reduction, may be effected by substances contained in the blood, which themselves undergo oxidation at its expense. Such a change certainly takes place in blood diluted and put aside, before putrefaction takes place, the spectrum being distinctly altered to that of purple cruorin, and being changed back again to that of scarlet cruorin, by agitation with air. A temperature as high as that of the blood in the body, facilitates these changes.

The possible mode of occurrence of such alternate changes in the blood in the systemic and the pulmonary capillaries, is illustrated by Stokes, by first reducing, or deoxygenating, a solution of scarlet cruorin, by means of a slightly alkaline solution of the protoxide of tin in tartaric acid, and then re-oxygenating it, by agitation of the altered coloured solution with air. If the mixture be now allowed to stand for two or three minutes, the colouring matter is again slowly deoxidised; by agitation it is once more oxidised; and so on for a number of times. In this experiment, the purple cruorin absorbs oxygen more readily than the salt of tin does; but afterwards, it slowly parts with oxygen to that salt.

In the same way, the purple cruorin, as it passes through the lungs, absorbs oxygen by a special affinity, and then in circulating through the systemic capillaries, it is partially deoxygenated, to supply the wants of the disintegrating tissues, by a so-called *parenchymatous respiration*; on returning to the lungs, it is once more reoxygenated.

The various alterations in the colour of the blood, noticed in different conditions, accord with this conclusion. Thus the blood is unusually dark as it returns from the muscles, and the depth of its colour is in exact proportion to the activity of those muscles, when, as we shall see, it also contains the most carbonic acid. On the other hand, the venous blood returning from glands in a state of active secretion, is of a bright scarlet hue; whereas, when the glands are inactive, it is dark (vol. i. p. 333; vol. ii. pp. 56, 350). In the latter case, the quantity of blood passing through the gland, is small; nutrition proper is going on, and a proportional quantity of carbonic acid is formed and taken up; whereas for active secretion, the conditions existing are, a larger supply of blood, with a proportionally less amount of deoxygenation. Again, it has been noticed that, at high temperatures, there is much less difference in the colour of the arterial and venous blood-current, and also a less amount of respiratory interchange; whereas, at low temperatures, the difference of colour is greater, and so likewise is the activity of the respiratory process. In anæmia, in the state of hibernation, and also in sleep, the venous blood has the same colour as the arterial; and both the pulmonary and the parenchymatous respiration are imperfectly performed. Lastly, in asphyxia and in cholera, the blood is exceedingly dark, and, in both diseases, contains unusually large quantities of carbonic acid.

A further result of these researches, is to show that the oxygen carried through the body by the blood, is, to a large

extent, actually chemically combined with it, *i.e.* with the cruorin of the red corpuscles, though some must be merely dissolved in the liquor sanguinis, and all must pass through that fluid, to enter and escape from the corpuscles. But that a certain proportion of the oxygen is retained in the liquor sanguinis, is shown by the fact, that the clot of dark venous blood assumes a bright hue when placed in the serum of arterial blood, or even of the scarlet venous blood returning from an actively secreting gland. It is uncertain whether any of the carbonic acid is specially attached to the red corpuscles; it would rather seem not. The coagulum of the scarlet venous blood from a gland, as well as that of arterial blood, becomes darkened, when placed in the serum of dark venous blood; so that carbonic acid certainly exists in the liquor sanguinis of venous blood. It appears to be partly dissolved in the serum, and is partly, perhaps, in a state of loose chemical combination.

Changes in the Fibrin of the Blood.

During the aëration of the blood in the lungs, and perhaps as a special result of the action of oxygen absorbed from the air, the amount of fibrin is increased in arterial, as compared with that in venous blood; a difference also exists in the coagulating power of the arterial fibrin, which forms a firmer clot than that of venous blood. The influence of oxygen, in increasing the amount of fibrin, has been shown, by causing rabbits to breathe pure oxygen for a short time, and also by inducing an unusual activity of the respiratory movements by means of electricity applied to the spine and chest. In these experiments, the quantity of fibrin in the arterial blood was increased respectively to 2·4 and 2·9 parts in 1000 of blood; whereas in the ordinary arterial blood, the proportion found was only 1·65 (Gardner). The fibrin is, of course, produced at the expense of some other albuminoid body, either globulin or albumen. Even out of the body, a substance somewhat like fibrin, though not positively determined to be fibrin, has been produced by transmitting oxygen gas (A. H. Smee), or ozone (Gorup-Besanez), through a solution of albumen.

Change in the Temperature of the Blood.

Numerous attempts have been made, to determine whether there be any difference, and if so, what difference, between

the temperature of the blood, before and after it has passed through the lungs. The older physiologists, and also some recent observers (Harley and Savory), have maintained that the blood in the left ventricle, is warmer, by from 1° to 2° than that in the right ventricle; and, in accordance with this, it has often been supposed that the oxygen combined directly with certain constituents of the blood in the lungs, to produce the whole of the carbonic acid given off in respiration. But it is now known that this latter supposition is incorrect. Many observers, moreover, have found that the blood in the left side of the heart, is not so warm as that in the right cavities, owing, as they maintain, to a cooling process, caused by the entrance into the lungs of air of a lower temperature than the blood, and by the evaporation of moisture from the internal pulmonary surfaces. This does not affect the general conclusion, that the venous blood returning from the limbs, is cooler than the arterial blood of the same parts. We shall revert to this subject in the Section on Animal Heat.

Changes in the Gases of the Blood.

It has been elsewhere noticed (pp. 165, 168), that the vapour of water, and also many volatile substances and gases, are readily *absorbed* into the blood by the lungs; and, indeed, one of the two chief phenomena of respiration, viz. the entrance of oxygen into the blood, illustrates the absorptive power of the pulmonary mucous membrane.

This absorption of oxygen from the inspired air, by the venous blood brought to the pulmonary capillaries, is associated with the evolution of carbonic acid, which escapes from that venous blood, and is added to the air about to be expired. These two joint interchanges of the gaseous elements of the air and of the blood, are essential steps in the conversion of venous into arterial blood. That the blood participates in these changes, is shown by the fact that venous blood contains less oxygen and more carbonic acid than arterial blood, which, on the other hand, contains more oxygen and less carbonic acid, as shown by the following table (Magnus).

	Oxygen	Carbonic acid
100 vols. of Venous blood . . .	5 vols.	25 vols.
100 vols. of Arterial blood . . .	10 vols.	20 vols.

It has also been found that the proportions of oxygen and

carbonic acid in venous blood returning from muscles at rest, are 7·5 and 31, and from muscles *in action*, 1·265 and 34·4; whilst in arterial blood the proportions are 17·3 of oxygen and 24·2 of carbonic acid (Sczelkow). According to Magnus, arterial blood contains twice as much oxygen as venous blood generally, whilst, in the special case of the blood from muscles, the proportion is at least as 2·3 to 1. Again, ordinary venous blood contains $\frac{1}{5}$ more carbonic acid than arterial, and that from muscles at rest, about $\frac{1}{4}$ more.

The interchanges of oxygen and carbonic acid between the air and the blood, which characterise respiration, have, through the researches of Dalton, Draper and Graham, received a partly physical and a partly chemical explanation. The elimination of urea and uric acid, by the kidneys, and of certain excretory ingredients of the bile, is accomplished by organic vito-chemical processes performed by certain special epithelial cells; but the absorption of oxygen by, and the elimination of carbonic acid from, the lungs, or other respiratory organ, are purely physical and chemical processes. These may, indeed, be imitated artificially out of the body; for, as already mentioned, if a moist bladder be filled with venous blood, and be suspended in atmospheric air or oxygen, the surface of the blood in contact with the bladder, soon becomes scarlet, and, during that change, oxygen is absorbed, and carbonic acid is given out from it, through the moistened bladder. It is remarkable that a function of the animal economy, so immediately and constantly necessary to life, is removed from the contingencies surrounding a purely organic process, and is brought into the sphere of physical and chemical actions. It is also worthy of remark, that the physical processes which accomplish the escape of the deleterious carbonic acid gas from the blood, and mix it with the air, also aid in the entrance of the essential purifying and stimulating oxygen from the air, into that fluid. The processes in question, are the *diffusion of gases*, or the tendency of dry gases to diffuse into each other, and their mutual diffusion when in a dissolved condition.

It was shown by Dalton, that, even when a light gas, such as hydrogen, is poured into a glass jar, on to the surface of a heavy one such as carbonic acid, or when a bottle full of the light gas, is inverted over another bottle containing a heavy gas, with their mouths applied to each other, the gases do not remain stationary, but are mutually transported into each other against gravity until they have intermixed in certain definite proportions. The facility with which they intermi-

is such, as to have been expressed by the phrase that each gas offers no more resistance to the other, than would an actual vacuum. This simple intermixture is called the *diffusion of gases*; it takes place with a definite energy, irresistible and invariable, when the conditions exist for its exercise. The force with which it takes place, and its extent, in any particular instance, are said by Dalton to be, generally, inversely as the densities or weights of the two gases respectively. Subsequent experiments on a most extended scale, enabled Graham to determine the true numerical expression, or law, of this diffusive power or energy of gases, viz. that the rate of diffusion of any gas, if dry and pure, is inversely as the *square root* of its *density* or specific gravity. Graham showed moreover, that this diffusion takes place through narrow tubes, and through porous substances, according to the same law, provided that the gases be dry and chemically indifferent to each other, and to the substance of the porous septum. On the other hand, when films of india-rubber or of shell-lac, moist animal membranes, or even soap-bubbles, are employed as the septa interposed between any two gases, diffusion still takes place, but then, not according to the above mentioned law, but under modifications dependent on the relative solubility of either gas, in the interposed septum. Lastly, experiments made by Draper, on gases in a state of *solution*, show that these still manifest mutually diffusive tendencies, although not according to Graham's law of their simple diffusion in a dry state. This moist diffusion of gases, has been termed *false gaseous diffusion*.

Both *simple* and *spurious* diffusion occur in aërial respiration performed by lungs or air sacs, but the latter only, in aquatic respiration, performed by gills or moist surfaces.

The breathing air in calm respiration, about 20 cubic inches, amounts to only $\frac{1}{9}$ th of the reserve and residual air together, 180 cubic inches, which are ordinarily retained in the lungs (see p. 433). Even in active respiration, it would only amount to about $\frac{1}{4}$ th, viz. 45 cubic inches. Hence, so small a displacement of the air in the lungs, at each inspiration and expiration, cannot directly influence the air contained in the remote air-cells, especially as the bronchial tubes constantly increase in their total capacity, from the trachea to the air sacs. The simple diffusion of gases here comes into play; for since, as we shall presently see, the last portion of air expelled in a long expiration, is richer in carbonic acid than the first portion, it is probable that the residual air, which is never expelled from the lungs, becomes increasingly richer in carbonic acid gas, and therefore poorer in oxygen, in the direction of the air-cells; hence, the diffusion of oxygen must take place from the larger bronchi, to which the pure air gains access, towards the air-cells; whilst carbonic acid diffuses itself in the opposite direction, from the air-cells towards the larger air-tubes. The respiratory move-

ments doubtless continually change the air in the lungs, and, as it were, partially ventilate the air-passages; but the energy and rapidity of the diffusive process, and its incessant operation, supplement their effects. The diffusion-process is accelerated by differences of temperature between any two gases, a condition constantly operating in respiration. Moreover, the pulmonary exhalation, which, in the air-cells and smaller air-tubes, exists in the form of vapour, likewise has a similar tendency to diffuse into the drier air in the larger passages. That this diffusion of carbonic acid gas, actually occurs in the lungs, may be shown, by steadily holding the breath, with the open mouth kept in communication with a bag, or other reservoir, holding a known volume of atmospheric air, when this latter is soon found to contain a readily appreciable quantity of carbonic acid. In apparent death or trance, when the respiratory movements are suspended, a minimum respiratory interchange of gases may thus take place, just sufficient to prevent the extinction of life. In the deepest stages of hybernation in animals, this also must be the mode of respiration. Under ordinary circumstances, however, the necessity for air, cannot thus be relieved; but successive respiratory movements are excited through the nervous system, in order to satisfy it.

But the entrance of oxygen into, and the escape of carbonic acid from, the blood of the pulmonary capillaries, from and into the air in the air-cells, is not explicable by simple diffusion: for this double process is one of *moist* or false gaseous *diffusion*. Both gases must be dissolved, as they pass in, or out of, the pulmonary tissues and capillaries; and the actual diffusion result depends first, on the relative solubility of the diffusing gases in the fluid of the natural moist septum through which they pass, and, secondly, on the special chemical affinities of those gases for the blood. The simple diffusion volumes of dry oxygen and carbonic acid, are in the proportion of 1174 to 1000, the oxygen, or lighter gas, having a higher diffusion volume than the carbonic acid or heavier one. But this proportion does not agree with the ratio of the oxygen absorbed to the carbonic acid evolved in respiration, which, according to the Table in p. 438, is as 1255 to 1000. The quantity of oxygen absorbed, is, therefore, not only greater than that of the carbonic acid evolved, but greater than that which the law of the diffusion of dry gases would account for. Again, the relative solubility of these gases in the *water* of the walls of the air-cells and capillaries, and in that of the blood, will not explain the differ-

ence; for carbonic acid is nearly 30 times more soluble in water, than oxygen, and, accordingly, it exhibits a far greater diffusibility through a dead moist membrane, instead of a less diffusibility, as occurs in actual respiration. It has been shown that recent blood, even at a temperature of 32° , retains from 16.8 to 19.8 volumes per cent. of oxygen; whilst water, at 60° , dissolves not quite 3 volumes. Furthermore, fresh blood deprived of its fibrin, at a temperature of 48° , absorbs 178 volumes of carbonic acid; whilst water takes up about 90 volumes. Hence, the proportion between the oxygen absorbed, and the carbonic acid exhaled from the blood in respiration, does not depend on the relative solvent power of the blood for those two gases, which is about as 1 to 10.

The remarkable affinity of blood for oxygen, is also shown by another calculation. The absolute quantity of carbonic acid, which is taken up by the blood, is larger than that of the oxygen. But in comparison with water, the special affinity of blood for oxygen, is much stronger than that for carbonic acid; for the quantity of oxygen absorbed by the blood, in comparison with that absorbed by water, is about as 18 to 3, or 6 to 1, whilst the quantity of carbonic acid absorbed by the blood, in proportion to that taken up by water, is only about as 178 to 90, or less than 2 to 1.

The total quantity of all the gases normally contained in 100 volumes of blood, amounts to somewhat less than 50 volumes, *i.e.* about half its own volume. This is less than it is capable of dissolving under artificial pressure, or through other means. Of these 50 volumes, about 12.5 are oxygen, 34.5 carbonic acid, and 3 nitrogen. Of 100 volumes of these mixed gases, the mean of several observations, however, gives 28.2 oxygen, 64.7 carbonic acid, and 7.1 nitrogen. Nitrogen, therefore, is also absorbed by blood in larger proportion than by water, which can only take up 1.5 volumes, whilst blood can be made to absorb 5 volumes, per cent.

It is plain, that both oxygen and carbonic acid are held in the blood, not merely by its solvent power, as was supposed from the experiments of Magnus, because he obtained those gases from the blood, by placing it under an air-pump, or by displacing them with streams of hydrogen; but that it is in part, and in great part, held in it by special chemical affinities. It is, moreover, evident that the absorption of oxygen by the blood, depends on one kind of chemical affinity, and that of carbonic acid, on another.

The *oxygen* is supposed almost entirely to enter into chemical combination, essentially with some constituent of the red corpuscles; for although, as shown by its relative effects on dark clots, the serum may contain variable quantities of oxygen, yet neither it nor the liquor sanguinis, can absorb more oxygen than pure water (Berzelius). That the oxygen is chemically combined is, moreover, inferred from the fact, that pyrogallic acid, which has an extraordinary affinity for this gas, does not withdraw it, when injected in solution into the blood, but appears unaltered in the urine. The extreme affinity of blood for *carbonic acid*, though partly due to the solubility of that gas in water, may be partly owing to some special absorptive power in the albuminoid or other organic constituents; but it is in a marked degree dependent on the carbonate, or perhaps rather on the phosphate of soda, which exists in considerable quantities in the liquor sanguinis.

The special affinity of the red corpuscles for oxygen, has been attributed to the iron contained in them, that element being supposed to be in the condition of a sesquioxide in the corpuscles of arterial blood, and of a carbonate of a protoxide in those of venous blood, the oxygen, it is said, being displaced by the carbonic acid, which preponderates in venous blood, and is the source of the carbonate above mentioned (Liebig). It has, indeed, been alleged that the fibrin is concerned in this transportation of the oxygen through the circulation, it having been supposed to be in a higher state of oxidation in arterial than in venous blood. But the spectrum analysis of the blood, proving that oxygen produces such remarkable changes in the relations of the cruorin to luminous rays, would lead to the conclusion, that it is this colouring substance of the red corpuscles, which is the real carrier of oxygen through the blood. Furthermore, it has been shown that the blood corpuscles even absorb ozone, which is oxygen in a peculiar condition, with great avidity, and yield it up to oxidisable substances when brought into contact with them; the cruorin is also specially concerned in this reaction. In animals provided with a distinct circulation and red blood, the activity of the respiratory function is closely related to the number and dimensions of the coloured corpuscles in the blood; for these are few and large in the Cold-blooded, whilst they are greatly increased in number and diminished in size in the Warm-blooded Vertebrata. The latter arrangement provides for an enormous multiplication of the surfaces of the corpuscles.

The entrance of oxygen into the blood, being thus due to the joint action of false gaseous diffusion and chemical affinity, the *escape of carbonic acid* gas from the blood, is perhaps dependent on diffusion only. The accumulation of this gas in the venous blood, owing to chemical processes to be presently mentioned, produces a greater tension in the carbonic acid in the blood, than in that present in the air of the air-cells; for it is proportionally much more abundant in the former than in the latter. Hence, an outward diffusion of the carbonic acid dissolved in the venous blood, through the moist walls of the pulmonary capillaries and air-cells, and its escape into the residual air, at the surface of the lining membrane of the cells. The carbonic acid thus dissolved in the blood, is chiefly contained in a state of solution in the liquor sanguinis, the red corpuscles having no special affinity for it. The absorption and evolution of nitrogen in the respiratory process, are accomplished also by moist diffusion.

Two points yet remain for consideration, viz.:—In what *part of the circulation*, and at the *expense of what constituents* of the blood and tissues, does the oxygen absorbed in respiration, become united with carbon, to produce the carbonic acid given off? The answer to these questions, constitutes an important part of the *theory of respiration*. Previously to the discovery of oxygen, nitrogen, and carbonic acid, all explanations of the respiratory process were necessarily vague. The earlier physiologists believed that the air—the source, as they deemed it, of the animal spirits—found its way through the lungs, and obtained an entrance, as such, into the so-called *arteries*.

Oxygen, or phlogiston, was discovered by Priestly and Scheele, in 1774. Black had already described what he called *fixed air*, and Rutherford had determined the existence, in air respired by an animal, of a peculiar *gas incapable* of supporting further respiration or combustion. Lavoisier named the gas first discovered by Priestly and Scheele, *oxygen*; by him also, the gas described by Rutherford, now more commonly known by the name of *nitrogen*, given to it by Chaptal, from its being contained in nitre, was named *azote* (*a*, not, and *zoe*, life), from its inability to support life, in respiration; lastly, Lavoisier demonstrated that the fixed air of Black, now shown to be produced alike by the action of acids on limestone, by combustion, fermentation, and respiration, contains the element *carbon*. These great discoveries were indeed the commencement of the modern science of Chemistry, and the foundation

of all true chemical theory; and Lavoisier himself, in combining and adding to the knowledge of his predecessors, at once applied the results to explain the respiratory process of animal life, and offered to science the first *theory of respiration*.

Lavoisier saw that the oxygen absorbed in respiration, united, in some way and somewhere, with carbon, to produce the carbonic acid evolved; he regarded the process as a sort of *combustion*, and supposed that the combination took place in the lungs, *i.e.* in the pulmonary capillaries, in which the obvious change from venous to arterial blood, occurs; the oxygen was thought to be there immediately transformed into carbonic acid, and then as immediately given off. But later inquiries have shown that this view must undergo modification. It was not known to Lavoisier, that both venous and arterial blood contain these two gases, and that both, therefore, circulate in the two kinds of blood; nor was he aware, that frogs made to respire nitrogen or hydrogen, that is, an atmosphere destitute of oxygen, continue for a time to exhale carbonic acid. The existence of both carbonic acid and oxygen, in solution, in the entire blood, shows that the combination of oxygen with some carbonaceous compound in the venous blood derived from the disintegrated tissues, does not take place in the lungs only; but that this union must occur in some other part of the body. Moreover, if this moist combustion took place entirely in the lungs, those organs should be very much warmer than any other part of the system; but, though some authorities, as already mentioned, maintain that the blood in the left ventricle, just returned from the lungs, is warmer than the blood in the right ventricle, the alleged increase of temperature has never been stated to be more than 2° ; whilst equally competent observers testify to an exactly opposite condition, as regards the temperature of the venous and arterial blood, before, and after, it has passed through the lungs.

According to another and more plausible view, the oxygen in the aerated blood, partly dissolved in the serum, but chiefly in loose chemical combination with the coloured substance of the red corpuscles, and perhaps with the fibrin, is conveyed in the arterial blood, to the systemic capillaries, where a certain loss of oxygen, and a nearly proportionate addition of carbonic acid, occur, the blood then becoming venous. On this supposition, the process of oxidation, or respiratory combustion, takes place not in the lungs, nor in the pulmonary capillaries, but in the system, in or near the systemic capillaries. This opinion is

in harmony with the fact, that the arterial blood once having acquired, in passing through the pulmonary capillaries, its special characters, amongst others, its bright colour, retains that colour, and, by presumption, its other qualities also, along the whole arterial system, only losing them, as it passes through the systemic capillaries. It is also consistent with other facts, already mentioned, viz. that, whereas arterial blood contains more oxygen than venous blood, venous blood contains more carbonic acid. If, as is asserted, the sugar found in the venous blood in the right side of the heart, is absent in the arterial blood in the left side of that organ, then a small portion of the oxygen absorbed in the lungs, or else some of that previously contained in the blood, must have united with that carbohydrate, and so have given rise to a certain amount of carbonic acid; but by far the larger proportion of the oxygen, probably passes on unchanged, in the arterial blood-current.

How much of the systemic process of oxidation which then takes place, occurs in the blood of the systemic capillaries, or in the tissues traversed by those vessels, is yet unknown. But there is reason to believe, that it happens in both situations. In the functional activity of *all* the tissues and glands, both secreting and ductless, but especially of the *muscular* and *nervous* tissues, constant nutritive changes are in progress; their life never stands still. Disintegration and renewal are unceasing; and the former always implies retrograde chemical metamorphoses, of which partial or complete oxidation is a characteristic phenomenon. The production of carbonic acid is one of the ultimate results. It is supposed by some, that here a repetition of the false or moist diffusion process, may take place, oxygen passing from the blood in the capillaries to the substance of the tissues and glands, whilst carbonic acid passes from them back into the blood. This interchange of the two gases at the systemic capillary circulation, constitutes the *parenchymatous respiration*, which, so far as the blood is concerned, is exactly the reverse of the pulmonary respiration; for in the former, the blood loses oxygen and gains carbonic acid, whilst in the latter, it loses carbonic acid and gains oxygen. This consumption of oxygen, especially by the nervous and muscular tissues, and its combination with their substance, are said to explain the so-called *stimulating* effect of oxygen upon those tissues, when they are actively engaged in their special offices in the living economy. The quantity of oxygen consumed, and of carbonic acid evolved, in any given case, are

found to be proportioned to the degree of activity of the nervous and muscular structures. The muscles especially, require a large supply of oxygen for their nutrition, but more for their effective action; the blood returning from a muscle at rest, as we have seen, contains 7·5 vols. per cent. of oxygen, but when in exercise, only 1·25 vols.; whereas arterial blood contains 17 vols. The prepared muscles of a frog, of course deprived of circulating blood, continue to absorb oxygen, and to give off carbonic acid, so long as their contractility is manifested (G. Liebig). Whether during life, this de-nutritive oxidation is entirely completed *in* the tissues, and the resulting carbonic acid is then transmitted from them, to the returning systemic blood, or whether some intermediate products of disintegration enter the blood, and are oxidated therein, or, lastly, whether both varieties of this combustive process take place during the ordinary nutritive changes in the tissues, is not well known. That substances properly belonging to the blood, are also oxidated within the systemic capillaries, cannot be denied; they are probably fatty matters and carbohydrates, or their derivatives, introduced into the blood from the food, constituting the so-called *respiratory food*; but it has hitherto been supposed that these are quite as actively oxidised in the lungs, and in the arterial blood-current generally, as in the systemic capillaries. But many have believed, and recent researches appear to show, that although the nutritive processes of the muscular tissue demand oxygen for the removal of disintegrated albuminoid and other materials, yet that in the active contraction of muscle, or in the development of *animal motion*, it is not, as was supposed, the muscular substance which wastes, by being more actively oxidised, but, rather, that some combustible substances in the blood, of the nature of respiratory food, either fatty matters or carbohydrates, then undergo oxidation, that this chemical action yields the carbonic acid formed in the blood of muscles, and that it is at once the source of the motive power exercised by the muscles, and of the heat evolved in the system. (See the Section on Animal Dynamics.)

In conclusion, then, it appears that the oxygen taken in during respiration, combines first, with the tissues during their action and nutrition, especially with the nervous and muscular tissues; secondly, with the partially effete matters of the blood, and, lastly, with the materials of the respiratory food. Hence, the carbonic acid, which is one of the ultimate products of these changes, is derived partly from the disintegrated

substance of the tissues, especially the nervous and muscular tissues, and partly from substances merely assimilated into the blood from the food. The oxidation of the respiratory food, appears to take place in the blood itself, partly in the lungs, but chiefly in the arterial blood-current, and, during muscular action, largely in the capillaries of the muscles. The oxidation of the substance of the tissues, may occur, partly, in the tissues themselves, outside the walls of the systemic capillaries, but partly, also, in the blood itself, into which certain intermediate effete products of disintegration may enter, and there undergo further oxidation, after the manner of the respiratory food.

The second point above suggested for consideration, viz. the *nature of the substances immediately oxidised*, must remain at present in obscurity. That they contain carbon is, however, certain. Some of this united with oxygen, forms the carbonic acid given off in respiration. They also contain hydrogen, frequently in excess of the quantity of oxygen atomically present in them; and then, by oxidation of this hydrogen, water must be formed in the system. But some carbon and some hydrogen escape perfect oxidation, appearing, combined with nitrogen and a little oxygen, in the urea, uric, and hippuric acids, and other nitrogenous excretory compounds. The sulphur contained in the albuminoid bodies, and the phosphorus present more especially in the phosphuretted fats of the red blood corpuscles and in the grey nervous substance, are likewise oxidised, at the cost of the oxygen taken in by the respiratory process, so as to form sulphuric and phosphoric acids, which appear in combination with alkalies or earthy matters, in the urine. The sulphur may be partly traced in the intermediate formation of taurin in the bile. With regard to the nitrogen contained in the so-called nitrogenous tissues, it is, as already mentioned, almost entirely accounted for, by the urea and uric acid—passing, probably, through intermediate chemical forms, such as creatin, creatinin, sarcin, glycin, allantoin, and others. Minute quantities appear to escape from the blood, as ammonia. The nitrogen exhaled from the lungs, and the small loss of that substance from the epidermis and the intestinal excreta, are not metamorphic, the former being derived from the air swallowed with the ingesta and the saliva, and the latter being contained in non-metamorphosed organised matter. Cholesterin is also a scarcely oxidised excretory hydro-carbon.

The great object, therefore, of the respiratory function, is to introduce oxygen into the living animal economy; this oxygen, by giving rise to numerous and incessant chemical changes, stimulates the animal tissues, combines with their substance and with the products of their disintegration, and ultimately converts them, either into crystalloid products, which can be readily excreted from the kidneys or skin, or into a gas—very soluble in water and in the blood—which can be readily displaced from the latter fluid, in the lungs or in other respiratory organs, by the stronger affinity of oxygen itself for a certain constituent of the blood. In accomplishing this, it also combines with certain constituents of the blood, assimilated to it from the respiratory food, and thus forms more of the same displaceable gas.

As an important collateral result, this process of oxidation, due to the respiratory function, produces *animal motion* and *animal heat*. In the Cold-blooded animals, in which respiration is comparatively feeble, and which consume but a small quantity of the carbohydrates, the quantity of force and heat engendered is relatively small; but in the Warm-blooded Vertebrata, much heat and force are manifested, and the quantity of respiratory food consumed, and the activity of the respiration are very great. The quantities of oxygen absorbed and of carbonic acid evolved, are much larger in the latter than in the former animals.

In animals provided with distinct blood and a complete circulation, the immediate effects of the respiratory process take place in that fluid, which is thus purified and rendered fit to maintain life. But the ultimate effect is still largely exerted on the tissues, the blood acting as a vehicle for the respiratory agent and its products. In the lowest members of the animal scale, respiration is equally necessary, and has similar ultimate results; but its effects are direct or immediate upon the tissues.

The relation between the chemical actions of the body and the amount of force and heat developed in it, also the manifestation of nervous power, and the evolution of electricity and light in animals, phenomena in which oxidation, at the expense of the oxygen absorbed in respiration, is likewise necessary, will hereafter require further consideration.

CONDITIONS WHICH MODIFY THE CHEMICAL PROCESSES OF
RESPIRATION.

The quantity of oxygen absorbed, and of carbonic acid eliminated, in the respiratory process, is modified by the frequency of the respirations, the number of times the same air is breathed over again, the temperature of the air, its degree of moisture, and its density; also by the conditions of age, sex, exercise, repose, or sleep, by the character and quantity of the food or drink, the period of the day or season, the state of health or disease, and by the use of remedial agents.

In *rapid breathing*, less oxygen is absorbed, and less carbonic acid is given off, at each respiratory movement, as if sufficient time were not allowed for the usual rate of mutual interchange of the two gases. With six respirations per minute, 5.5 per cent. of the expired air has been found to be carbonic acid; with 24 respirations, 3.3 per cent.; and with 96 respirations per minute, only 2.6 per cent (Vierordt). But although in slow breathing, more oxygen is absorbed, and more carbonic acid is exhaled at *each respiration*, yet, in a given time, as shown by multiplying the quantity exhaled by the number of respirations, the absolute quantity of the gases absorbed and exhaled, is increased by rapid breathing. In *deep inspirations*, the interchange of gases is said to be proportionally less, when compared with the quantity of air; but the total amount of interchange is greater, because the volume of air inspired and expired, is so much larger. The *last portion of air* expired, in all cases, contains less oxygen and more carbonic acid, than the first portion; the former, no doubt, containing air coming from the finest air-tubes, close to the air-cells, in which the actual absorption and exhalation occur.

The relative *purity or impurity of the air*, likewise affects the result; as when the same air is breathed over and over again, and so becomes more or less charged with carbonic acid. Thus, in an experiment in which 300 cubic inches of air were repeatedly breathed for a period of three minutes, only 9.5 per cent. of carbonic acid was found in it; the total quantity being 28.5 cubic inches, or 9.5 cubic inches per minute. In the same person, with fresh air at each inspiration, the quantity was 32 cubic inches per minute. However often the same air was respired, it was never found to contain more than 10 per

cent. of carbonic acid (Allen and Pepys). These results are caused by the increasing difficulty offered by the accumulation of carbonic acid in the air of the air-passages, to the escape by moist diffusion, of the carbonic acid from the blood into the air-cells, and to its simple diffusion through the air of the air-passages.

The effect of an *increased temperature* of the air, is to diminish, and that of a *lower temperature*, is to increase, the quantity of carbonic acid exhaled by the lungs. Between the temperature of 47° and 67° , *i.e.* with a difference of 20° in the external temperature, a variation has been observed in the quantity of carbonic acid exhaled, of 2.5 cubic inches per minute (Vierordt). At very low temperatures, the quantity of carbonic acid exhaled, may even be more than twice as great as that given off at very high temperatures. A sudden increase of temperature, produces a marked immediate effect, *viz.* a decrease of 2.75 cubic inches per minute, for 16° of elevation of temperature, but this is not subsequently so regularly maintained (Dr. E. Smith). The absorption of oxygen is, of course, inversely affected.

The *density of the air*, also influences the chemical changes dependent on respiration, their activity being increased when the density of the air is diminished.

A *moist atmosphere*, the temperature being the same, greatly favours in animals, the exhalation of carbonic acid; moreover, the influence of moisture is so great, as to neutralise, at high temperatures, the effect of such temperatures in diminishing the exhalation of that gas (Lehmann). The exact hygrometric state of the air, ought always, therefore, to be taken into account, in experiments on the composition of expired air. The great influence of moisture, may account for some of the discrepancies between the results of different observers.

As regards *age*, the quantity of oxygen absorbed and of carbonic acid exhaled, increases generally, in both sexes, to about the thirtieth, and then remains stationary to the fortieth year, after which it diminishes, so that at seventy, the amount only slightly exceeds that proper to the age of ten years. The influence of *sex*, as might be expected from the greater size and activity of men, is, after the eighth year, shown in the proportionally larger amount of oxygen absorbed, and of carbonic acid exhaled, in that sex. In the male also, the increase due to age, continues progressively up to the thirtieth year, at which period, it is stationary; whereas in the female, the gradual

increase stops at the age of puberty, and the quantity remains stationary until about forty, when it once more increases for a time, before the diminution dependent on old age, begins. The smaller absolute quantity of carbonic acid exhaled in childhood, is, nevertheless, very large, in proportion to the weight of the body, in accordance with the high activity of the nutritive function, and with the large consumption of food at that period. The *size* of the body, in different adults, produces a correspondent result on the total quantity of carbonic acid exhaled. The development of the muscular system, however, produces a greater effect, than that which depends on the mere height or weight of the body, or on the dimensions of the thorax.

Exercise, as might be expected, increases the quantity of carbonic acid exhaled, not only whilst it is being taken, but also for a short time afterwards. The increase may equal one-third of the amount exhaled during rest, and this may continue for one hour after the cessation of exertion. This result depends both on a greater quantity of air being breathed, and on an increased percentage of carbonic acid in the expired air (Vierordt). Other observations show even a greater relative increase, for in walking two and three miles per hour, the quantities, 18.1 grs. and 25.8 grs., were about two or two and a half times as great as the normal amount in the sitting posture; at the tread-wheel, the quantity fluctuated between 42.9 grs. and 48.6 grs., that is, from about four and a half to five times as great, the pulse and the respiration being, of course, greatly accelerated (E. Smith). Prolonged exertion producing fatigue, diminishes the exhalation. Much less carbonic acid is exhaled during the *night* than in the *day*. During *sleep*, the amount given off is considerably diminished, in correspondence with the more superficial and slower character of the respiratory movements of the chest, with the cessation of the ordinary actions of the muscular and nervous tissues and of the usual metamorphoses of the respiratory food, and with the smaller loss and production of heat. In experiments performed in air-tight chambers, the diminution per hour in sleep, was about one-third of the normal quantity (Scharling). According to other estimates, the quantity exhaled, in a given time, during profound sleep, is about one-half that of the average quantity in the same time during the day.

The *period of the day*, influences the quantity of carbonic acid exhaled, quite independently of the condition of sleep or wakefulness. The ratio in a like time of the night and day,

being as 1 to 1.25 (Scharling), or as 1 to 1.8 (E. Smith). Taking the whole day of 24 hours, the smallest quantity is exhaled in the middle of the night, and the largest in the middle of the day; a slight increase occurs at sunrise, and a prolonged and constant diminution after 9 o'clock in the evening (E. Smith). The difficulty of resisting the effects of severe cold, between midnight and sunrise, is well known. A *seasonal* influence on the products of respiration, has also been noticed: the maximum product occurs in spring (April and May), and the minimum at the end of summer (September), a gradual increase occurring in early winter (October, November, and December), and a gradual decrease in early summer (June, July, and August). Hence, heat, as the result of seasonal changes, equally with artificial heat, diminishes the quantity of carbonic acid exhaled, and climatic cold increases it; moreover, it was found by Barral, that the daily quantity of carbon exhaled by the skin and lungs, was, in winter, upwards of 5,000 grains, and in summer only about 3,700 grains. But neither temperature alone, nor this, added to the effects of atmospheric pressure, account for the seasonal changes (E. Smith). It may be remarked, however, that the hygrometric condition of the air in the above researches, was not taken into account, but this, as shown by Lehmann, is of the highest importance; the period of increase corresponded with the wet months, and that of decrease with the dry months of the year.

Food generally increases the absolute quantity of carbonic acid given off from the lungs, whilst *fasting* has the opposite effect, the proportion of carbonic acid in a given quantity of the expired air, being, however, greater during starvation. Thus, in a person six feet high, in whom the average quantity of carbon exhaled, when at rest, with ordinary diet, was 7.85 oz., the daily quantity exhaled whilst fasting, was 5.9 oz.; the diminution produced by fasting for the 24 hours, being rather more than one-fourth the usual quantity exhaled when taking food (E. Smith). The quantity exhaled in fasting, sinks to a certain line, which has been named the *basal line*, below which, in health, it does not descend; but prolonged starvation ultimately diminishes it. The influence of food has been shown, by an increase after breakfast of one-fourth the previous quantity, and after dinner of about-two thirds (Scharling); the chief increase noted by Dr. Smith, was after breakfast and tea, and not after early dinner. Thus, the average quantity of

carbonic acid exhaled, by a certain person, being 20·6 cubic inches (9·77 grs.) per minute, the quantity during continuous fasting being about 14 cubic inches (6·61 grs.), and the maximum and minimum quantities in the working day with food, 22 cubic inches (10·43 grs.) and 14·2 cubic inches (6·74 grs.), the increased exhalation after breakfast and tea was from 4·2 to 6·3 cubic inches (from 2 to 3 grains), and after early dinner only from 2·1 to 4·2 cubic inches (from 1 to 2 grains). The different effect of different kinds of food and drink, as observed by Dr. Smith, is, in some respects, remarkable; all nitrogenous foods increase the exhalation of carbonic acid; and so does any mixture of nitrogenous matters with the carbohydrates, such as is found in bread, oatmeal, and milk; but pure starch has scarcely any effect; pure fat seems even to diminish the quantity of carbonic acid evolved, though pure sugar increases it. Tea, coffee, and cocoa cause an increase more sudden and marked than that produced by any other substances experimented with; pure alcohol also increases the quantity; but of the spirits ordinarily in use, rum increases the quantity, brandy and gin diminish it, whilst whisky varies in its effects; wine and ale increase it, whilst the volatile or aromatic ingredients of both spirits and wine, seem to lessen the quantity exhaled. Distilled water has been found to diminish the exhalation of carbonic acid. The opposite effects of different alcoholic fluids, such *e.g.* as rum and brandy, are referred by Dr. Smith to the separate action of the alcohol, sugar, aromatic substances, and nitrogenous bodies in each of those fluids respectively; and the different effects of weak alcoholic liquors, and of pure alcohol, have been explained by supposing, that in the former case, the alcohol may act chiefly by stimulating the respiratory changes; whilst in the latter, it may interfere with the oxidation of the ordinary constituents of the body. Habitual drinkers, usually, accumulate fat.

From the preceding facts, it would appear that the constituents of food, do not act in proportion to the quantity of carbon they contain; but that some specifically excite the respiratory interchanges, apparently by increasing the processes of oxidation in the body, and by augmenting the depth of the respirations, or the quantity of air inspired. Two substances, identical in composition, sugar and starch, act differently; the former exciting respiratory interchange, the latter not doing so. Milk, especially when new, is a more powerful excitant even than a

purely albuminoid substance. The nitrogenous foods increase the quantity from 1 to 2·1 cubic inches (from $\frac{1}{2}$ to 1 gr.), mixed nitrogenous and hydro-carbonaceous foods give an increase of about 4·2 cubic inches (2 grs.) per minute; milk, a perfect mixed diet, 4 cubic inches (nearly 2 grs.) per minute; spirits of wine 2·1 cubic inches (1 gr.); rum 3 cubic inches (about $1\frac{1}{2}$ gr.); ale and stout 2·1 cubic inches (1 gr.); whilst tea, coffee, and cocoa increase the evolution of carbonic acid from 3 to 6·3 cubic inches ($1\frac{1}{2}$ to 3 grs.) per minute (E. Smith). Certain substances, such as sugar, alcoholic fluids, tea, and coffee, produce their effect very quickly, reaching their maximum within half an hour; whilst flesh, bread, oatmeal, and milk act later, their influence enduring as long as two hours and a half (E. Smith). Lastly, the effect of a high diet on one day, may affect the respiratory changes, as well as the excretion of urea, on the following day, imparting, as it were, a somewhat durable stimulus to the system.

The amount of carbonic acid exhaled, is diminished in all chronic and organic diseases of the lungs, in hectic conditions, and in cholera; whilst it is increased in chlorosis, in which the number of the red corpuscles is diminished. The proportion of carbonic acid in a given amount of expired air, is increased in certain exanthematous diseases, as in measles, and especially in smallpox, in which it is nearly doubled; whilst, on the other hand, it is reduced about one-half, in typhus fever. The absolute quantities exhaled in these and other diseases, have not been sufficiently investigated.

The effects of remedial agents, generally, on the absorption of oxygen and exhalation of carbonic acid, have likewise yet to be scientifically determined. The inhalation of the vapour of chloroform and ether, diminishes remarkably the escape of carbonic acid from the blood; and this constitutes an accessory cause affecting the nervous system. In the treatment of diseases by change of climate, the increased respiratory interchange which is induced by cold, and the diminished oxidation which takes place in higher temperatures, should be considered, as well as the great influence of atmospheric moisture, in increasing the exhalation of carbonic acid, and of a dry air, in diminishing it. It is possible that, in some degree, the hygienic value of a dry climate, such as Egypt, in the treatment of diseases of exhaustion, may depend upon the comparatively limited amount of waste and oxidation of the tissues generally.

In hibernating animals, the quantity of oxygen absorbed

and carbonic acid evolved, is, like the respiratory movements themselves, reduced to a minimum, or, it is said, the respiratory interchanges are even absolutely arrested.

Effects of Breathing other Gases than Air.

As already mentioned, many gases and vapours of volatile substances, are introduced into the system, by absorption from the pulmonary mucous membrane. Chloroform, ether, camphor, and turpentine, thus produce their characteristic active results on the system; so likewise do tobacco smoke, the smoke of the datura stramonium, and the vapour of mercury. The gaseous combinations of hydrogen with other elements, such as arseniuretted, phosphuretted, sulphuretted, and carburetted hydrogen, are especially and directly poisonous. The arseniuretted hydrogen is the most powerful, less than one-tenth of a grain, when inhaled, having proved fatal to Man. Sulphuretted hydrogen stands next in potency, air containing from one to three per cent. having been respired without much inconvenience to Man, though much less destroys animals. Carburetted hydrogen, or marsh gas, the fire-damp found in coal mines, is still less active as a poison, but destroys life when present in large proportions. The vapours of nitric, nitrous, sulphurous, and hydrochloric acids, as well as those of ammonia, which are compound bodies, and those of bromine, iodine, and chlorine, which are simple bodies, are likewise positively injurious when inhaled into the lungs, causing direct irritation of the mucous membrane, and producing decompositions of a special kind when taken into the blood. Besides causing an increase of the mucous secretion, intense bronchorrhœa, serous inflammation, and often permanent cough, they frequently produce, through reflex nervous action, violent spasm of the glottis, and so may cause *asphyxia* or death from *suffocation*, without entering the air-tubes; sometimes death results from œdema of the glottis. There is one gas, a compound of nitrogen with oxygen, the *nitric oxide*, or *laughing-gas*, which, when inhaled for some minutes, produces a state of temporary intoxication, and, at the same time, maintains respiratory chemical changes, at the expense of the oxygen contained in it, the products of respiration being, in such a case, carbonic acid with a large excess of nitrogen. By a long continuance of the experiment, insensibility, and,

nitrous

as has been shown on animals, actual suffocation, probably from the carbonic acid, may be produced.

Besides these directly irritant and poisonous gases, there are some which are only indirectly injurious, being in themselves inert and innocuous. Thus, snails have been kept in pure *hydrogen* for a long time, and frogs as long as fourteen hours, without any injurious effects; and *nitrogen* is equally harmless to frogs (Collard de Martigny, Müller, Bergmann). In the experiments on frogs, carbonic acid is exhaled, for a time, in as great, or even greater, quantity than if the animals had breathed atmospheric air; more is excreted in hydrogen than in nitrogen. The total quantity of carbonic acid, so given off, is, however, limited, doubtless because no more oxygen can be absorbed; the lungs of the frog have been usually emptied of air, by compression or the use of the air-pump, and the only oxygen left in the animal, was that in the blood or the tissues. Some of the hydrogen and nitrogen seems to be absorbed, but only in small quantity. The exhalation of carbonic acid in these cases, must be owing to the successive moist and dry diffusion taking place into the hydrogen or nitrogen; and the diffusive force, in the former gas especially, would be much greater than that into air. In the case of Warm-blooded animals, only the newly-born or very young can support such an experiment, without the rapid extinction of life; but they may live a short time, and yield carbonic acid to the artificial atmosphere of hydrogen or nitrogen. Fully-grown Birds and Mammalia, expire rapidly in pure hydrogen or nitrogen; the symptoms being instantaneous difficulty of respiration, gasping, loss of muscular power, and, at the end of two or three minutes, cessation of the heart's action; the lungs are found engorged with venous blood. The animals, indeed, are asphyxiated from the deprivation of oxygen, of which they require a larger and more constant supply, in comparison with the young of the same species, or with Cold-blooded animals. That the nitrogen is not in itself injurious, is obvious from the large proportion of it—about four-fifths—in ordinary atmospheric air; and that the same is true of hydrogen, is shown by the fact that, if this gas be mixed with oxygen, in the same proportions as nitrogen and oxygen exist in the air, animals live and breathe in such a mixture, without the least inconvenience.

From all that has preceded, it is evident that of the two gases in the atmosphere, the oxygen is the active ingredient in respiration; for nitrogen alone, as we have seen, causes suffocation.

Hence *oxygen* has been named *vital air*. Considered in reference to its office, it is a supporter of *life*, or of the proper animal functions; but, as regards the *body* itself, it is a destructive, not a constructive, agent, operating constantly in its disintegration and oxidation, in the various processes of animal life. The proper medium for healthy respiration, is pure atmospheric air, which contains, besides a minute trace of carbonic acid, four-fifths of nitrogen, and only one-fifth of oxygen. But an addition to the normal quantity of oxygen, is of more or less importance. Twice or three times the usual quantity in air, at first causes no apparent inconvenience, and no special change in the products of respiration; but it is probable that, after a time, certain injurious consequences would ensue, though experiments are wanting to determine the point. Pure oxygen, however, is highly injurious; the vital functions are stimulated as if by a fever; the pulse and respiration are increased in frequency; after an hour, insensibility gradually comes on, complete coma then ensues, and death occurs in from six to twelve hours. On examination of the animal, the heart is found pulsating violently, although the motion of the diaphragm is arrested. The blood, after death, is of a bright colour in the veins, as well as in the arteries; the mucous membranes are red; the blood coagulates quickly; oxygen has evidently been absorbed in large quantity; the blood in the systemic capillaries is no longer properly changed to venous blood; and, on the other hand, the presence of over-oxygenated blood in the nervous centres which govern respiration, lessens their activity, which is called into play apparently by the stimulus of a certain quantity of carbonic acid in the blood. The symptoms produced by breathing oxygen, are rapidly alleviated by respiration in atmospheric air.

Of the three compound gases containing carbon, viz. carburetted hydrogen CH_4 , carbonic oxide CO , and carbonic acid CO_2 , *carbonic oxide* is the most poisonous. This gas, which is produced by the imperfect combustion of carbon, is given off, together with carbonic acid, in the fumes of burning coke or charcoal. The addition of 5 per cent. of this gas to air, is sufficient to make it irrespirable, and to cause death, and it is this gas, rather than the carbonic acid, which produces fatal results, in suicide by charcoal fumes. In these fumes, however, besides the carbonic acid and the carbonic oxide, there are ammoniacal salts, an empyreumatic oil, sometimes sulphurous acid, watery vapour, nitrogen, and traces of

free oxygen. The symptoms produced by smaller quantities of carbonic oxide in air, are, giddiness, faintness, headache, convulsions, and irregularity of the pulse; the freest inspirations, or insufflations of pure air, or of diluted oxygen, are essential for recovery at such a crisis. When death ensues from the breathing of carbonic oxide, the blood is not found dark, as in asphyxia from carbonic acid, but even the venous blood is of a bright red hue, and the properties of the corpuscles are permanently modified; for they exhibit no further changes on exposure to oxygen or to carbonic acid.

Carbonic acid being a natural product of the respiratory process, its injurious effects upon animal life, possess an interest greater than that which attaches to those of other gases. The quantity of this gas in ordinary air, is about 4 parts in 10,000, $\frac{1}{2500}$ th part, or .04 per cent. In air once breathed, the proportion rises to about 4 per cent, *i. e.* $\frac{1}{25}$ th part, or 400 parts in 10,000, a corresponding quantity of oxygen being simultaneously removed. If this air be respired a second time, a much smaller portion of carbonic acid is added to it, and still less, at each subsequent respiration. When air contains about 10 per cent. or $\frac{1}{10}$ th its volume, of carbonic acid, when one-half of the normal quantity of oxygen, has likewise disappeared, it is irrespirable, and fatal to man. Warm-blooded animals have been found to die in an atmosphere containing from 12 to 18 per cent. The symptoms of poisoning, may be said to begin with even a much smaller proportion in the air, even with as little as one-third per cent. For a time, no marked symptoms are observed, but after a certain interval, there occur headache, sense of fulness in the temples and occiput, giddiness, muscular prostration, oppression of the chest, difficult respiration, palpitation of the heart, subjective, disturbed sensations, such as singing noises in the ears and flashes of light, faintness, delirium, then drowsiness, unconsciousness, convulsions, coma, and death. Sometimes vomiting occurs, and occasionally death ensues from apoplexy. On examination after death, the cerebral vessels are found congested, and serous exudations to be present in the ventricles and at the base of the brain; sometimes clots of blood are found in the substance of the brain. Carbonic acid is the choke-damp of mines.

Asphyxia.

When a person is completely immersed in an atmosphere of almost *pure carbonic acid*, as in brewers' vats, in cellars in which wine is fermented, or in caverns, such as the Grotto del Fane, death occurs much more rapidly; the glottis is sometimes spasmodically closed, and respiration is as completely arrested by this impediment to the passage of air, as it is in strangulation, or in any other mechanical form of suffocation. Even if the glottis should remain patent, the entire absence of oxygen from such an atmosphere, would produce suffocation almost as speedily; for twenty seconds is the extreme time during which the breath can be held by voluntary effort; so that suffocation might be said to commence at the expiration of that brief period. In any case, the form of death, which so rapidly ensues, is that by *asphyxia*, the essential characters of which, are, loss of muscular power and consciousness, cessation of the movements of the chest, and then of the pulsations of the heart, with accumulation of blood in the right side of that organ, and in the whole venous system, so that even the skin becomes livid. The blood remains a long time fluid.

The mode in which death occurs from asphyxia, whether caused by compression of the chest and abdomen, by direct suffocation from external strangulation, internal choking, or spasmodic closure of the glottis, or whether produced indirectly by immersion in some irrespirable gas, or in water, by paralysis of the respiratory nervous centres, or by narcotic poisonings, is somewhat complicated. The respiratory interchanges of carbonic acid and oxygen, between the blood in the pulmonary capillaries and the air in the air-cells, diminish or cease; the venous blood, reaching the lungs, no longer gives off its carbonic acid, and the pulmonary capillary circulation is more or less quickly stopped. The *forward* effects of this, are, that the left side of the heart receives, at first, imperfectly aerated blood, and then little or no blood at all, so that the functions of the brain and nervous centres, of the muscular system, and of the heart itself, all of which require, for their maintenance, a due supply of arterial blood, gradually or rapidly cease; ultimately, the left side of the heart and the arteries, accommodating themselves by their muscular contractility and elasticity, are nearly or entirely emptied, or contain but very small quantities of dark non-aerated blood. On

the other hand, the *backward* effects of the arrested circulation in the pulmonary capillaries, are ultimately, to distend the right side of the heart, and the entire venous system, with very dark blood. The stagnation of the blood in the pulmonary capillaries, which is the first stage of the fatal process, has been attributed to some direct influence of the carbonic acid on the blood corpuscles; for the circulation in the transparent parts of animals, may be arrested, by subjecting the capillaries to the action of carbonic acid; moreover, as the red corpuscles of the blood undergo enlargement when acted upon by this gas, it has been supposed that these bodies may then obstruct the capillaries mechanically (Wharton Jones). It has also been suggested that there exist, in the healthy state, certain local attractions and repulsions between the walls of the pulmonary capillaries and the currents of the non-aërated and the aërated blood respectively, connected with the respiratory interchanges of the carbonic acid and oxygen, which are essential to the onward movement of the blood-current.

In the slower forms of asphyxia, indicated by the more gradually-developed cerebral symptoms, the stagnation of the blood in the pulmonary capillaries, is preceded by a simple retardation of the blood-current in them; but the entire blood is defectively aërated. Hence this fluid, owing to its abnormal condition, passes imperfectly through the systemic capillaries; the arteries and the left ventricle become somewhat distended, and the heart for a time beats more powerfully and more frequently, as if to overcome this resistance. But the activity of the nervous centres and muscular system is soon diminished, in proportion as the blood becomes less and less aërated; at length, both are completely paralysed, the senses fail, consciousness is lost, the respiratory nervous centres lose their power, respiration becomes laboured and much interrupted, general convulsions ensue, and respiration ceases. The contractile power of the heart itself, becoming diminished, it beats more slowly, and at length ceases to contract. The left ventricle not only no longer receives its appropriate stimulating blood, but even loses its power of rhythmic contraction owing to the poisoning of the blood in the nutrient vessels of the heart and its nervous ganglia; whilst the cessation of the action of the right ventricle, is chiefly the result of over-distension, for venous blood is its proper stimulus, and the contractility of that side of the heart is retained, for more or less time, after it has ceased to beat spontaneously. If, indeed

he state of over-distension be relieved by puncturing the right auricle, or the great veins, the right ventricle will again begin to contract; whilst the left ventricle may be once more excited by duly arterialised blood. By some, it has been supposed that the obstruction to the pulmonary capillary circulation, is due to the mechanical non-expansion of the lungs, but it also occurs in asphyxia produced in animals made to respire nitrogen, in which case, the lungs are not contracted. Moreover, the vascular pulmonary obstruction, which is caused by asphyxia, is relieved by the inhalation of oxygen very rapidly, as compared with the gradual dilatation of the arterial system, when any mechanical obstruction to the circulation of the blood in them, has to be removed. The question has arisen, whether in asphyxia from the inhalation of carbonic acid, the result is due to the diminished supply of oxygen, or to a directly poisonous effect of the carbonic acid itself. The latter conclusion is supported by the fact that when animals are made to breathe an atmosphere consisting of carbonic acid, mixed with oxygen in the same proportion as exists in air, or even in much greater proportion, they are still quickly destroyed by asphyxia. It has been found, moreover, that a diminution in the proportion of oxygen, increases the poisonous effects of the carbonic acid; where the quantity of oxygen is reduced to 16 or $10\frac{1}{2}$ per cent., death speedily ensues, even though the carbonic acid is constantly being removed; but if the oxygen be maintained at its ordinary proportion of 21 per cent., the ill effects of carbonic acid are not manifested more rapidly, even though as much as 20 per cent. of that gas be present in the respired air. A still more positive proof of the directly poisonous influence of carbonic acid, is furnished by the following singular experiment. One bronchus of a tortoise was tied, and the animal lived apparently without inconvenience; the respiration, accomplished by one lung, being temporarily sufficient. But if, by special arrangements, ordinary air was allowed to enter one lung, and carbonic acid the other, through their respective bronchi, the animal soon died, the introduction of carbonic acid into the system, being the sole difference in the two conditions. This experiment also proves that carbonic acid may, in certain conditions, not only not escape from the lungs, but may actually be absorbed by them (Rolando).

Suspended Respiration and Animation.

The length of time which different animals, or Man, can survive without respiration, varies, according to many conditions, chiefly referable to the relative degree of activity of the animal functions in any given case, but sometimes also to special provisions. The more active the nutritive and respiratory processes, and the greater the development of heat, the sooner does death by suffocation ensue. Thus, cold-blooded animals, with the feebler activity of all their functions, have less need for air than warm-blooded animals, the water-newt, *e.g.* frequently remaining, even in its active summer life, a quarter of an hour or more under water; whilst frogs and lizards have been kept, in experiments, for years without food, enclosed in porous stones, or buried in earth; but when they are hermetically enclosed, they sooner or later die. Warm-blooded animals and Man, on the other hand, are rapidly asphyxiated. Hybernating Mammalia are able to live, in their peculiar torpid condition, with a supply of air so defective, that they would die asphyxiated in it, during their active summer condition. Newly-born animals, being less dependent on the perfect state of respiration, survive submersion for much longer periods, especially when their temperature is low; rabbits, under such circumstances, having survived as long as 26 minutes, and puppies even 50 minutes; young guinea-pigs, however, do not seem to possess this immunity. Even full-grown animals resist the injurious effects of submersion in water, for a longer time than usual, when their temperature has been previously reduced as low as 64° , but not lower (Brown-Séquard). Again, it has been observed, that full-grown warm-blooded animals die sooner from drowning, than from simple apnœa caused by immersion in nitrogen or hydrogen, by choking, or by strangulation, the more rapid fatal result in drowning, being due, not only to the deprivation of air, but to the partial filling of the air-passages and air-cells with water, and to the poisonous effects of carbonic acid. Thus, the average time in which rabbits, suddenly deprived of air, cease apparently to live, has been found to be 3 min. 25 sec.; in the case of dogs, the time is 4 min. 5 sec.; the action of the heart, however, was maintained for 7 min. 10 sec.; moreover, the animals thus deprived of air, could be restored to life after 3 min. 50 sec. On the other hand, an immersion in water for only $1\frac{1}{2}$ or 2 minutes

usually rendered recovery impossible. Lastly, if the trachea of an animal be divided and plugged, so that the water may be excluded from the air-passages, and it be then submerged, even for four minutes, it may recover its respiratory power (Rep. Med. Chir. Soc.). Animals subjected to a diminished atmospheric pressure under the receiver of an air-pump, are asphyxiated, sometimes, perhaps, owing to the liberation of gases in the blood of the small pulmonary bloodvessels.

In a few Warm-blooded Mammalia, destined for an aquatic life, as, *e.g.* in the Cetacea, there exist special provisions in the presence of arterial and venous plexuses or diverticula, in which the blood may accumulate during their submergence. The retia mirabilia, or wonderful networks of the arteries, contain a supply of oxygenated blood, which is employed, as required, by the submerged animal; whilst the large venous plexuses receive a like quantity of deoxygenated blood. Whales can remain upwards of an hour beneath the water. Certain diving birds possess similar diverticula of both arteries and veins.

In Man, under ordinary circumstances, the breath can be held for about 20 seconds: but after an ordinary inspiration, the period of endurance without air, may be prolonged to 25 seconds. If, however, a single forcible expiration be made, and then a deep inspiration be taken, the period may be extended to about 33 seconds. If five or six deep expirations and inspirations be made, one after the other, so as to clear the lungs as completely as possible of used-up air, and then a deep inspiration be taken, from one and a half to two minutes may be allowed to pass without inconvenience from want of air, with the exception of slight giddiness at first. This fact it is useful to remember in passing through rooms filled with smoke or on fire, or on entering such rooms, or descending a vat, or diving in water to save the life of another. In entering an apartment on fire, or filled with smoke, it is better to stoop or creep along the floor, as the air in that situation is cooler and less pungent; but in the case of wells, brewers' vats, or sewers, the entrance of which, for a time, is most hazardous, there is no great elevation of temperature, and the lower strata of air are the most poisonous. By practice, persons may accustom themselves to an interruption of the respiratory process for three or four minutes, without loss of consciousness, or other serious consequences, three minutes being the ordinary limit attained by the skilled pearl-divers of Ceylon.

Some of these divers use a small *spring-clip*, made of horn, which they slip over the end of the nose, the instant before they enter the water. This, on the one hand, prevents the escape of air from the thorax through the nose, and, on the other, the entrance of water through the same passage; without this contrivance, the diver must hold the nose with one hand, which would limit his powers of search and prehension at the bottom of the sea; moreover, if the nostrils are not closed, the muscles of the glottis and of inspiration must be kept incessantly strained, or an irresistible expiratory effort would take place, and expel some air from the chest. With this protection on the nose, however, the diver has only to keep the mouth closed; the inspiratory muscles are not required to act, and the contents of the chest are mechanically retained.

Persons who have been submerged for four or five minutes, are rarely restored to life, and sometimes, often owing, doubtlessly, to the entrance of water into the air-passages, persons who have been submerged scarcely a minute, cannot be resuscitated.

A submergence of five minutes, is almost certainly fatal to Man, still recoveries have occasionally taken place after much longer periods, even a quarter of an hour, and it is said after half an hour or more. In such cases, however, it is believed that just before, or at the moment of immersion, *syncope*, from some cause or other, has taken place. In this condition, or in a state of *trance*, the heart beats feebly, or scarcely at all, the respirations are weak and shallow, and life may be said to be interrupted, or so feebly maintained, that it may be continued as well under the water, as above it; venous blood is not propelled through the system, so that the nervous centres are not poisoned by carbonic acid; and, unless the temperature of the water be very low, the vitality of the respiratory nervous centres, of the muscles of respiration, and especially of the heart, may be suspended, but not altogether destroyed. Such a condition of *syncope* or fainting, may be produced, either by a severe blow causing concussion of the brain, by other physical shocks to the body, by sudden fright, or violent passion. For these reasons, attempts at the resuscitation of apparently drowned persons, should always be resolutely persevered in even under most unfavourable circumstances.

Certain methodical rules have been laid down, by means of so-called *artificial respiration*, for the recovery of drowned persons; and, with the exception of such parts of those rules, as relate to the removal of water from the mouth and nostrils, and

the replacing of cold and wet, by warm dry clothing, similar instructions would apply to the recovery of persons suffocated in brewers' vats, wells, and sewers, and also to those asphyxiated in the administration of ether or chloroform. In the case of persons mechanically strangled or choked, the external or internal cause of obstruction in the air-passages, must of course be first removed. The earlier rules, published by the Royal Humane Society, for the recovery of drowning persons, were improved by Dr. Marshall Hall; but the most simple and convenient are those of Dr. Silvester, which have been incorporated with the present rules of that Society.

RULES OF THE ROYAL HUMANE SOCIETY.

Treatment to restore Natural Breathing.

RULE 1.—*To maintain a Free Entrance of Air into the Windpipe.*—

Cleanse the mouth and nostrils; open the mouth; draw forward the patient's tongue, and keep it forward: an elastic band over the tongue and under the chin will answer this purpose. Remove all tight clothing from about the neck and chest.

RULE 2.—*To adjust the Patient's Position.*—Place the patient on his

back on a flat surface, inclined a little from the feet upwards; raise and support the head and shoulders on a small firm cushion or folded article of dress placed under the shoulder-blades.

RULE 3.—*To imitate the Movements of Breathing.*—Grasp the patient's

arms just above the elbows, and draw the arms gently and steadily upwards, until they meet above the head (this is for the purpose of drawing air into the lungs); and keep the arms in that position for two seconds. Then turn down the patient's arms, and press them gently and firmly for two seconds against the sides of the chest (this is with the object of pressing air out of the lungs. Pressure on the breast-bone will aid this). (The Silvester method.)

Repeat these measures alternately, deliberately, and perseveringly, fifteen times in a minute, until a spontaneous effort to respire is perceived, immediately upon which cease to imitate the movements of breathing, and proceed to INDUCE CIRCULATION AND WARMTH.

Should a warm bath be procurable, the body may be placed in it up to the neck, continuing to imitate the movements of breathing. Raise the body in twenty seconds in a sitting position, and dash cold water against the chest and face, and pass ammonia under the nose. The Patient should not be kept in the warm bath longer than five or six minutes.

RULE 4.—*To excite Inspiration.*—During the employment of the above method excite the nostrils with snuff or smelling-salts, or tickle the throat with a feather. Rub the chest and face briskly, and dash cold and hot water alternately on them.

Treatment after Natural Breathing has been restored.

RULE 5.—*To induce Circulation and Warmth.*—Wrap the patient in dry blankets and commence rubbing the limbs upwards, firmly and energetically. The friction must be continued under the blankets or over the dry clothing.

Promote the warmth of the body by the application of hot flannels, bottles or bladders of hot water, heated bricks, &c., to the pit of the stomach, the armpits, between the thighs, and to the soles of the feet. Warm clothing may generally be obtained from by-standers.

On the restoration of life, when the power of swallowing has returned, a teaspoonful of warm water, small quantities of wine, warm brandy and water, or coffee, should be given. The patient should be kept in bed, and a disposition to sleep encouraged. During reaction large mustard plasters to the chest and below the shoulders will greatly relieve the distressed breathing.

In the recovery from *drowning*, or from other forms of *asphyxia*, the various phenomena which characterise the production of that state, are, as it were, reversed or undone, beginning at the re-establishment of the flow of blood through the pulmonary capillaries. On the introduction of air into the lungs, by the artificial imitation of the respiratory movements, oxygen is once more absorbed by, and carbonic acid given off from, the venous blood reaching those organs; these renewed chemical changes in the blood, induce again its onward motion through the capillaries into the pulmonary veins; thence it flows on, more or less oxygenated, into the left side of the heart, which resumes contractions of sufficient strength to propel this oxygenated blood into the nutrient arteries of the heart and its ganglia, as well as into the muscular and nervous systems generally. In this way, the rhythmic power of the heart itself, and the excitability of the respiratory nerves, the nervous centres, and muscles, are restored, and, subsequently, consciousness, perception, and volition. In the meantime, moreover, the restoration of the capillary circulation in the lungs liberates the blood previously pent-up in the right cavities of the heart, gradually unloads those cavities, facilitates, more and more, at each moment, their free action, and so by degree empties the over-distended venous system. The freer return of the blood from the systemic capillaries, being thus permitted that part of the circulation also is relieved, the lividity and coldness of the surface of the body, are removed, and simultaneously, the vigour of the left side of the heart being increased, the flow of properly oxygenated blood, throughout the

whole system, and life itself is restored. The action of the air upon the blood in the capillaries of the skin, may slightly assist in these favourable changes; for the lividity of the skin sometimes diminishes, even when life is not restored.

It has been found by Dr. Richardson, that artificial respiration, by direct inflation of the lungs of animals, fails to restore the pulmonary capillary circulation, if the beats of the heart have actually ceased, an event which usually occurs after five minutes. Insufflation of the lungs with hot air, is more stimulating to the heart, but yet not adequate to restore the pulmonary blood-current. The employment even of oxygen or ozone, mixed with the air, is useless, unless the heart is still beating. Galvanism will revive the respiratory movements, but, unless the heart is still beating, it fails to re-establish the motion of the blood through the lungs. In short, if once the blood-current in the pulmonary artery and its branches, be interrupted, the blood corpuscles in the small vessels speedily coalesce, and then the increasingly feebler contractions of the heart, merely propel blood into the trunk of the pulmonary artery, but not through the lungs. Artificial respiration by insufflation, or even by Silvester's method, must not be attempted, or continued, when the feeblest natural respiratory movements are discernible. The introduction of air into the lungs must then be very gentle; the temperature of the air should, if possible, be as high as 120° , and never below 60° . Galvanism, being exhaustive of, as well as stimulating to the respiratory muscles, should either be employed for a limited time, or should be perhaps avoided. Certain experiments, on what Dr. Richardson terms *artificial circulation*, encourage him to hope, that means may ultimately be found of restoring life, if the blood is not actually coagulated, an event which does not usually take place before twenty minutes, and may not do so within an hour, in unopened and unexposed bloodvessels. Injections of oxygen into the circulation, or of peroxide of hydrogen into the trachea, may excite the heart or muscular system generally, but they do not restore the circulation through the lungs. The injection of vapour, and of hot water at the temperature of 120° , into the veins, excites the action of the heart in an extraordinary manner; whilst that of warm defibrinated and deoxygenated blood has no effect. Galvanism, applied to the heart jointly with artificial respiration, excites both sides of that organ, and, for a time, restores the pulmonary circulation. The forcible injection of blood into the jugular *vein*, with

the view of overcoming the resistance to the motion of the blood in the lungs, entirely fails in its object. On the other hand, suction of the blood, by aid of a syringe introduced into a large *artery*, draws some of that fluid through the pulmonary capillaries, in an oxygenated state, and on its being reinjected into the artery, so as to reach, amongst other parts, the walls of the heart through the coronary arteries, effectually re-establishes the pulmonary circulation, and all the functions of the body. The injection of the blood back into the artery, in a pulsatory or interrupted manner, revives the action of the heart most completely from its quiescent, cold, and partly rigid state, even *one hour and five minutes* after death. These interesting experiments, though not yet of practical application in the treatment of asphyxiated persons, serve to corroborate the generally-received opinion, that an essential fact in asphyxia, is the retardation, and subsequent arrest, of the movement of the blood through the pulmonary capillaries, and point to the relief or removal of that condition, as the turning-point of success in all attempts at resuscitation.

Effects of Breathing Impure Air.

Instances have occurred, in which the carbonic acid exhaled by large numbers of persons crowded together in small apartments, has been most destructive to human life. The Black Hole of Calcutta was a room only 18 feet square, having two small windows; into this apartment, 146 prisoners were literally crammed, and, during one night, 123 of them perished. The cruelty of an enemy, in 1756, was scarcely more disastrous than the ignorance of the captain of an Irish passenger steamer, in 1848, who, during a storm, confined under closed hatches, in a small crowded cabin, 150 passengers, of whom 70 died in the night.

But carbonic acid produces injurious effects, even when it exists, in the air, in quantities too small to cause asphyxia; as for example, when not more than *one* per cent. is present. Thus in ill-ventilated apartments, the presence of an excess of carbonic acid in the atmosphere, here, interferes with the proper oxygenation of the blood; for, as already mentioned, less and less carbonic acid is exhaled, as the proportion of that gas increase in the inspired air. Headache, oppression of the senses, lassitude of the muscles, and languor of the mind, are the results the oxidation of the effete matters of the blood, is imperfect.

performed or prevented, and they accordingly accumulate in that fluid; the pulmonary and cutaneous exhalations become still more loaded with such substances, and, together with the carbonic acid itself, and the ordinary exhalations from the skin and lungs—with which the air in such confined apartments, is already infected—produce still more depressing effects upon, and ultimate injurious consequences to, the system.

During each minute, an ordinary adult inspires and expires 360 cubic inches of air, exhales 14·4 cubic inches of carbonic acid, and absorbs at least 15 cubic inches of oxygen; this renders 150 cubic inches of air totally irrespirable; for, as already mentioned, this condition is arrived at, when half the normal quantity of oxygen (30 parts in 150) is replaced by carbonic acid. But in order that the air of any room, should be fit for continuous respiration, a much greater change must be effected in it, than that of merely replacing, minute by minute, the 360 cubic inches of air breathed in that time. For the 4 per cent. of carbonic acid contained in it, is sufficient, with the concurrent loss of oxygen, to deteriorate a much larger quantity of air. It is 100 times more than that which is present in common air, for this is only ·04 per cent.; and therefore, even when diluted with 100 times its volume of ordinary air, the mixture would still contain twice the normal quantity of carbonic acid, viz., ·08 per cent., or 8 parts in 10,000; this is about the average quantity in the air of certain large manufacturing towns. For such a dilution, 36,000 cubic inches, or more than 20 cubic feet of air would be required. Owing, however, to the rapid, spontaneous, dry diffusion of the carbonic acid, a less degree of actual dilution is sufficient for the purposes of healthy respiration; and it has been variously computed, that from 4 to 10 cubic feet of air per minute, which last-named quantity, with the respired air, would yield an atmosphere containing 12 parts of carbonic acid in 10,000, are needed for each person, in sleeping or sitting apartments, schools, courts, theatres, workshops, factories, barracks, work-houses, or prisons. Hospitals, especially for surgical cases or fevers, require at least double that quantity. Much depends on the temperature of the air, for a higher temperature requires a more rapid change. Moreover, besides the removal of carbonic acid and the renewal of oxygen, it is of the utmost moment that other pulmonary and cutaneous exhalations, which contain volatile organic matter and ammoniacal salts, should be diluted, oxidated, or removed. If the products of

the combustion of artificial lights, especially of gas, enter the air of the room, a still further allowance of fresh air is necessary.

Were it not for the law of diffusion of gases, the evils arising from overcrowded and ill-ventilated rooms, would be much greater. In the air of a very close room, which had been occupied by 500 people, and in which fifty candles had been burning, Dr. Dalton found, after it had been shut up for two hours, one per cent. of carbonic acid. But Dr. Roscoe has shown that in theatres, the percentage is usually $\cdot 0321$, and in schoolrooms $\cdot 331$; indeed, in no rooms did he ever find more than $\cdot 5$ per cent., owing, as he remarks, to the constant diffusion and interchange of air through the crevices and openings at the doors, windows, and fire-place. Furthermore, in proof of the rapidity and importance of the diffusion of carbonic acid in the air, he found that the percentage of carbonic acid was nearly uniform in every part of an occupied room, at the same time. Nevertheless, this accidental diffusion is insufficient for the proper change of the air in a crowded room. The escape and entrance of quantities of air, are indispensable for the removal of the noxious products thrown off from the living body, and for the renovation of the atmosphere. This is to be accomplished, consistently with warmth and comfort, by *artificial ventilation*.

Besides this motion of the respired air, and its replacement by fresh air, a certain actual breathing space should be allowed for each person occupying private sleeping apartments, or for those attached to barracks, workhouses, prisons, and, especially, to hospitals. The day rooms being more or less constantly opened may be smaller. The practice of architects and builders, up to a recent date, was to allow not less than 800 cubic feet of space for each person; but this is too little, especially in infirmaries and hospitals, in which 1,200 cubic feet per head are not considered too much, and for military hospitals in warm climates, as much as 2,500 cubic feet per head have been recommended. The importance of sufficiency of breathing space and of ventilation, in sleeping apartments, *can hardly be over-rated*, especially when we reflect that, even in health, the bedroom is occupied, from first to last, nearly 8 hours out of the 24, or nearly one-third of our existence. In hospitals and infirmaries, the same room is too frequently occupied both day and night.

The deterioration of health, from neglecting to sleep in a

pure air, is shown in many ways. Many competent authorities attribute the deposition of tubercle in the lungs, *i.e.*, the early stage of phthisis, partly to inadequate respiration, and to imperfect oxidation of the constituents of the blood and tissues. Consumption appears to have been engendered in the *Quadrumana* confined in the small overcrowded monkey-houses of the London and Parisian Zoological Gardens; but after increased accommodation and proper ventilation were secured to those animals, tubercular disease almost disappeared from amongst them. The small, close, sometimes doubly-glazed houses in Wales, contrast with the open dwellings of the inhabitants of Skye, and so does the prevalence of consumption in the former, with its rarity in the latter, districts. At an infant school at Norwood, a great mortality occurred amongst the children, clearly dependent on imperfect ventilation. Similar experience might be derived from every large town in the kingdom, provided facts were always duly recorded and understood. In the infant hospital at Dublin, 2,944 children died during four years, under a system in which ventilation had been utterly neglected; whilst in a similar period, during which many improvements in this respect, were made, the mortality fell to 279. Sometimes the injury may consist in a lowering of the strength of the system, which exposes it to the attacks of impending epidemic or zymotic diseases. The effete matters retained in the blood, must deteriorate the fluids of the body, or escaping into the air, they may form an organic nidus for the development of some diseases, or they may ferment, become putrescent, and so favour the multiplication and spread of poisonous fomites. Such effete matters may even undergo decomposition within the body. The lowered condition of health thus induced, favours the continuance of the evil practice of breathing impure air; for in this depressed state of the respiratory and other functions, the need for fresh air is less felt, and habit reconciles the senses, and dulls the perception, to the effects of the suicidal practice of inhaling an atmosphere poisoned by oneself. Persons accustomed to hot, close, unventilated rooms, loaded with a vitiated atmosphere, do not recognise either by smell, or by the sensations of enfeebled bodily health and infirmity, the effects of the impurities which they breathe. Moreover, they often believe themselves, and are regarded by others, to be in an average state of health; but the onset of an epidemic, or of a contagious disease, reveals their want of power to resist morbid influences. As a most serious

predisposing cause of disease and mortality, during such visitations, the overcrowding of rooms, whether large or small, public or private, is fully recognised.

The overcrowding of the population in parts of towns or villages, is also very inimical to health. This is doubtless partly to be explained by the fact, that it is the poorer classes, less well provided for, in every way, which occupy such neighbourhoods; it is also partly due to the closer proximity of the inhabitants to each other, and to their increased liability, from this circumstance, to communicate diseases to one another. But the increased accumulation, within a limited space, as in towns, or in the immediate neighbourhood of dwellings, as in villages, of the excreta, and of the waste animal and vegetable matters of the food, which constitute, when undergoing decomposition, sources of contamination to the air, cannot be here disregarded. Indeed, it has been shown that whereas, in the open country near Manchester, the quantity of organic matter in the air, is only 1 grain in 200,000 cubic inches, in the confined and overcrowded districts within that city, the proportion is, 25 grains in the same quantity of air.

The open ditches for drainage, and the heaps of garbage and refuse, in villages, and the uncleansed sewers, defective drains, and untrapped water-closets and sinks, in cities and towns, by admitting the escape of foul air into the environs, the lanes, the streets, or the houses themselves, are serious causes of insecurity to health. Sewer-atmosphere usually contains sulphuret of ammonium, or ammonia and sulphuretted hydrogen, frequently carburetted hydrogen, and besides these, it is loaded with *organic matter*, decomposing or putrescent, mixed with the spores of *fungi*, and with the minute living organisms known as *bacteria*, or, at any rate, with the organisable material in which these are generated. A house into which such an atmosphere is conducted, by an untrapped sink, or other defect, resembles, when closed at night, an inverted bell-jar over an open gas-pipe, or a receiver specially connected with the sewer, which acts as a retort for the evolution of poisonous vapours. It is necessary to exclude such chances of contamination of the air inside a dwelling-house; and to prevent also the contamination of the atmosphere in the immediate vicinity of the dwelling, from which the internal supply for ventilation is derived. This is the immediate sanitary purpose of a perfect system of sewerage and drainage. Water is, for large cities certainly, and perhaps also, wherever available, the most cleanly, and convenient vehicle for carrying away the excretory products of the inhabitants: the sewers should themselves be ventilated. Great care is needed to prevent the sewage matter from contaminating wells, or other sources of drinking-water; for water is, thus, as easily, and much more insidiously, contaminated than air. Earth closets are suitable for the country.

It seems probable, though but little is certainly known on these subjects, that zymotic diseases, whether contagious or epidemic, spread themselves, at least to a great extent, through the *air*, and enter the body through the lungs; moreover, it is possible that the agents which cause them, have, if not an organic *germinating*, at least a chemical *self-multiplying* property, and that impurities, whether in *solid bodies*, in *water*, or in *air*, may form a nidus for such increase, or growth.

The mortality from epidemic and contagious diseases, both local and

neral, has been repeatedly demonstrated to be proportional to the pure condition of the atmosphere of houses or localities. On the other hand, a decrease in the amount and severity, of zymotic diseases, and in the rate of mortality induced by them, has been shown to follow sanitary improvements in different towns. In the city of Salisbury, the annual average mortality during eight years previous to the complete drainage of the city, was 27 in 1,000; whilst in the succeeding eight years, it was reduced to 21 in 1,000. In the city of Ely, with a population of 6,176 persons, living in 1,200 houses, the average annual death rate, for the seven years from 1843 to 1849 inclusive, was 26 per 1,000; in the year 1851, public sanitary works were brought into operation, and, for the seven years from 1851 to 1857, the death rate was reduced to $19\frac{1}{2}$, whilst in the last of those years, it was only 19 in the 1,000. Besides securing a larger supply of better water, 4,000 cubic yards of cesspools were filled in, and trapped water-closets were substituted; but, in 1857, 200 houses were yet unconnected with the public drainage, and the pigsties were left, as being too sacred to be touched. It is noticeable, that, whilst the death rate in this city, was reduced, subsequent to the sanitary improvements from 26 to 19, the annual death rate in the surrounding country was still 21, in 1857 (William Marshall). The annual mortality at Pau, one of the healthiest places in France, varies from 28 to 23 per 1,000; the highest actual mortality in England is 45, the lowest is 11, and the average, 22, per 1,000. A comparison with these figures, indicates the sanitary position of the city of Ely. The death rate of 11 per 1,000, is regarded as representing the *inevitable annual mortality* of this country; the additional deaths beyond that, constitute the *preventible mortality*, dependent almost entirely on zymotic diseases, the ravages of which might be more or less controlled by sanitary improvements. It has been quite recently shown, that one important and unexpected result of public sanitary improvements, is a marked diminution in the number of deaths from phthisis; this is probably due to the better system of drainage, and to a general elevation of the health of the inhabitants (Dr. G. Buchanan).

A supply of *pure water* to a town, is of immense sanitary as well as economical importance. It facilitates the cleansing and purification of both dwelling-houses and streets, and thus assists in the improvement of the air. It substitutes a wholesome beverage, for that contained in unclean tanks or butts, or for the water of surface wells, which from the soakage of filth, from pigsties, stables, or cesspools, is frequently converted into a deleterious, or even directly poisonous, drink. Impure water may act, by slowly introducing into the system, organic matter undergoing more or less change, and probably, capable of deteriorating directly, or indirectly, the composition of the blood, and thus ultimately lowering the health, and rendering the body more subject to the influence of zymotic agents. At other times, the water may act as the *receptacle*, the *nidus*, and the *vehicle*, of such zymotic poisons. The evidence collected first by Dr. Snow, in the epidemics of cholera in Lambeth, and afterwards by the Rev. H. Whitehead, in St. James's, Westminster, and by others, at Epping, and elsewhere, concerning the influence of water in intensifying, or probably in communicating cholera, is too strong to be resisted, though it has met with but a tardy acceptance.

The use of water, free, if possible, from organic impurities derived

from dwellings, or from other sources, is as essential to good health as pure air. Filtering and depositing beds fairly purify water, on a large scale; but in private houses, if any doubt exist as to the character of the drinking water, special filtration through animal charcoal, or through the magnetic oxide, or the carbide of iron, or if this be too expensive, boiling, and subsequent agitation or exposure to a pure air, are desirable precautions.

In regard to public improvements, sanitary science consists in the perfection of cleanliness of the *town*, the *house*, the *water*, and the *atmosphere*. The cost of such improvements, and the great question of the utilisation of sewage, have also an economical aspect. For the national welfare, it is essential that sanitary work should be done; but it is not necessary that it should be directly profitable, or even free from cost.

THE ORGANS AND FUNCTION OF RESPIRATION IN ANIMALS.

As already stated, respiration is usually either *aërial*, or *aquatic* according to the medium in which an animal is fitted to live; but, in a few cases, both kinds of respiration are possible, as in the true *Amphibia*. Examples of *aërial*, and of *aquatic* breathers, are met with in the *Vertebrate*, *Molluscos*, and *Articulate Sub-Kingdoms*; but in the *Molluscoidea* and *Annuloida*, as well as in the *Cœlenterata* and *Protozoa*, the respiration is, in all cases, purely *aquatic*. The respiratory organs afford no grounds for classification.

Aërial Respiration.

The general principles, physical and chemical, on which this kind of respiration is performed in animals, are the same as those which govern the respiratory process in *Man*; but the organs concerned, vary according to the animal, and exhibit wide departures from the form and structure of the apparatus in *Man*, as we descend in the scale.

Vertebrata.—In all *Mammalia*, the respiratory apparatus is similar in plan, and even in detail, to that of the human body. There is a complete thorax with movable walls, separated from the abdominal cavity by a perfect diaphragm, and containing lungs suspended freely in pleural chambers, resembling, in all essential particulars, those of *Man*. The respiratory movements are performed in the same manner; their frequency also has a general relation to that of the pulse. The respirations are fewer, like the beats of the heart, in the larger *Mammalia* than in the smaller ones, these latter requiring relatively, more frequent changes of air in the lungs, to maintain sufficient respiratory action for the development of heat, and for other purposes in their economy. In the *Carnivora*, the lungs are relatively much larger than in the *Herbivora*. The right lung is usually the larger. In the horse and elephant, and in most *Cetacea*, they are simple in form; but more commonly they are divided into lobes; usually on the left side, these do not exceed three, and, on the right, five lobes.

In *Birds*, besides a typical symmetrical arrangement, as to position and size, important peculiarities in the respiratory apparatus are met with. The thorax and abdomen form but a single cavity, there being usually a rudimentary diaphragm only, which is spread out upon the base of the lungs, as in some *Reptiles*. In the ostrich tribe, however, the

diaphragm approaches, by its greater development, the Mammalian character, and in the Apteryx, this musculo-tendinous partition is quite perfect. The *thoracic walls* are constructed on a modified plan. The sternum, here expanded into the large breastbone, which gives attachment to the muscles of flight, forms the greater part of these walls, and even supports the abdominal viscera; whilst the ribs, which have a peculiar angular joint between their sternal and vertebral portions, occupy proportionally a smaller part. The absence of the diaphragm, and the difficulty of expanding a thorax thus constructed, by any active inspiratory movement, have led, as it were, to a complete reversal of the mechanism by which the air is drawn into, and expelled from, the chest. In Mammalia, and in Man, inspiration is an active, whilst expiration is, to a large extent, a passive movement; but in Birds, expiration is active, whilst inspiration is chiefly, if not entirely, passive. In expiration, the large sternum is drawn towards the vertebral column by muscular effort; the ribs are approximated, and bent at the above-mentioned angles, and so the thoracic part of the thoraco-abdominal cavity and therefore its contained lungs, are compressed, and air is driven from them. The expiratory muscles now cease to act, and the sternum, chiefly by the elastic resilience of the bent ribs, being drawn from the vertebral column, pressure is removed from the surface of the lungs, and air is inspired; the expansion of the lungs, is probably favoured by the contraction of the incomplete diaphragm, which is attached to their base. The condition of the thorax and lungs when at rest, corresponds with the state of distension, whilst active breathing begins by an effort to force air from the chest, and not to draw it in, as is the case in Mammalia. The *lungs* of Birds, are somewhat flattened, and fixed to the back of the thorax; they are relatively smaller than in Mammalia; their lobules are very distinct, each having its own bronchial tube and bloodvessels. Their interior is extremely subdivided, or cellular; the sacculi or cells thus formed, are at first supported by delicate cartilaginous trabeculae; but some open into the ultimate air-cells. These cells are small; whilst the capillaries upon them are exceedingly numerous, and their network very close, and owing to the frequent communications between neighbouring clusters of air-cells, and to other minute arrangements, come into relation with the air on both sides. These capillaries when injected, seem to be varicose, and even to project into the air-cells, in such a manner as to appear naked, or not covered by mucous membrane; this view is adopted by some, though, more probably, an exceedingly delicate membrane exists upon them.

The high temperature, the active habits, and the rapid waste of tissue in Birds, are associated with a corresponding activity of the respiratory function. These animals absorb a larger amount of oxygen, and exhale more carbonic acid, in relation to their weight, than the Mammalia; they are also much more dependent on a due supply of pure air, than the latter, and are much more quickly asphyxiated. Two supplementary anatomical conditions, peculiar to Birds, must more or less aid in their active respiration. First, there are usually found in the neck, thorax, and abdomen, and even in the limbs, membranous bags, named *air-sacs*, into which the air gains access by extensions from certain bronchial tubes, which reach to the surface of the lungs, and there communicate with the thoracic or pleural air-sacs, from which other communications

extend to the abdominal, and remaining air-cavities. These air-sacs are highly elastic, have a few plain muscular fibres in their walls, and are lined by a fine, moderately vascular, and partially ciliated mucous membrane. Secondly, in many Birds, most of the *bones* are hollow and are filled with air. In certain Mammalia, some of the bones of the face and cranium, contain air; but, in most Birds, besides these bones, the vertebrae and sternum, and even the long bones, which, in Mammalia, and in the early condition of the Bird, contain marrow, such as the clavicle, humerus, and femur, and even the merrythought and shoulder bones, are in the full-grown Bird, occupied with air, which finds access to their interior, by special membranous canals leading from the adjacent air-sacs. When the trachea is tied, respiration may be performed for a time through an aperture made in the arm-bone. These cavities in the bones, are lined with a membrane which, as compared with that of the air-sacs, is highly vascular. In Birds, killed suddenly, or destroyed slowly by drowning, the air in the air-sacs and bones, is often charged with from 8 to even 15 per cent of carbonic acid (Dr. Davy); respiratory interchanges of oxygen and carbonic acid, probably therefore here take place between the air and the blood, and these cavities must be regarded, not so much as supplementary, as sub-respiratory chambers, for the increase of the surface of absorption and exhalation. But their importance, in this respect, has perhaps been exaggerated. An equal extension of respiratory surface, if that only were needed in the economy of the Bird, might have been obtained by a trifling enlargement of the lungs themselves; the membrane lining the cavities of the bones, is not so vascular as a respiratory membrane usually is, whilst that of the capacious air-sacs, is still less so; moreover, there are some Birds which have no air in the long bones, or even in other bones; such exceptions occur in various Orders, chiefly, however, amongst the smaller Birds, and some aquatic species; lastly, the Apteryx has no air in any of its bones, and is even destitute of air-sacs, excepting the pleural chambers, in this respect being quite singular.

The high temperature of Birds, has probably some other explanation than the presence of these sub-respiratory air-chambers. As already mentioned, vol. i. p. 236, these air-sacs, and the air-cavities in the bones, cannot much diminish the weight of a Bird in the air, by the relative temperature of their contents, but they may aid in flight, by their distending, and giving fixity to the thorax, which is the base of action for the wings; they may also, by the different pressure which is exercised upon them during flight, act as a sort of pneumatic apparatus for the movement of air through the lungs, at a time when ordinary expiration is necessarily interfered with.

In *Reptiles*, the highest of the Cold-blooded animals, the respiratory apparatus is well developed; but in comparison with the Mammalia and Birds, the lungs, though even larger in proportion to the size of the body, are not nearly so minutely subdivided in their interior, as in the Warm-blooded Vertebrata. Besides this, neither the arrangements of the heart and large bloodvessels, nor the structure of the thorax, are so well adapted for the perfect distribution of the blood to the lungs, and for the continuous introduction of fresh air into the air-cells; lastly, the pulmonary capillaries are not so numerous.

The greatest diversity is met with in these animals, as regards the

structure and the mobility of the thoracic walls. In the Saurians, as in the Crocodiles and Lizards, the *thorax* is constructed somewhat after the Mammalian type, with movable ribs and a small imperfect sternum; in the Chelonia or Turtles and Tortoises, the walls of the thorax are completely immovable, being fused, as it were, into the carapace and plastron; whilst, in the Ophidians or Serpents, the thoracico-abdominal cavity is very capacious and expansible; the exceedingly numerous ribs are disconnected in front, owing to the complete absence of a sternum; they are extremely movable, and have powerful muscles attached to them. In the higher Saurians only, is any trace of a diaphragm found; no such structure exists in the Chelonia, or Ophidia. The act of respiration is never performed in these animals, by an inhaling movement. In this respect they resemble Birds; but they differ from these even more remarkably, for they all force air into the chest, by an act somewhat similar to that of deglutition. Air being drawn into the pharynx, by the depression of the hyoid apparatus and its attached soft parts, the posterior nares are then closed, and, by an elevation of the same parts, the air is forced down through the glottis into the trachea. Expiration depends chiefly on the elasticity of the lungs, indeed, almost entirely so in the Chelonian Reptiles, being assisted only by the abdominal muscles; whereas, in the Saurians and Ophidians, it is aided by the intercostal muscles and the resiliency of the walls of the chest. The *lungs* of Reptiles, fig. 115, are large in proportion to their bodies, and in the Chelonia, are attached to the sides of the chest. They are sometimes cellular, and sometimes saccular. When they are cellular, as in the Saurians, and the Chelonians, 3, the cells are few, and form large alveolar spaces, presenting, on a section, a spongy structure, the bronchial tubes being soon lost in the wide cellules which communicate freely with one another. In certain Saurians, the two lungs are unequally developed; and, in the lower forms, the lungs become much elongated, and smoother in their interior. In the Ophidians and snake-like Saurians, it is the rule to find only a single, long, cylindrical, sac-like lung, in a fully developed state, viz. the right one; the left lung is either slightly, or not at all, developed. The single lung, when distended, reaches through the greater part of the cavity of the body, and is saccular; the portion nearest to the trachea, however, has its sides marked with numerous alveolar depressions or imperfect cellules, supported by a cartilaginous framework, and having vascular walls; the larger portion of the sac has smooth and slightly vascular membranous parietes, fig. 115, 1. Even in the Crocodiles and Turtles, owing to the large size of the cellules, and to their slightly subdivided form, the pulmonary mucous surface for the capillary network, is comparatively small; in the Serpents, it is even proportionally less. Besides this condition, the less perfect nature of the inspiratory mechanism, the small quantities of air slowly and feebly impelled into the lungs, and the arrangements of the vascular system, imply a less active respiration, in accordance with their usually slower life and habits. In the aquatic Ophidia, the buoyancy of the body, is greatly aided by the size of the lungs, especially in the Turtles, the shell of which is of great weight.

In the *Amphibia*, which include the Frogs, Toads, Newts, Sirens, Proteus, and others, the anterior walls of the thorax are defective, and there is no diaphragm. The air, as in Reptiles, is drawn through the

nostrils into the pharynx, by the depression of the hyoid apparatus and floor of the throat, and is propelled through the glottis, by the subsequent elevation of the same parts. The lungs of the Frog, fig. 115, 2, may be described as subcellular; the internal subdivision of their surface into cells, is more simple than that of the Saurian Reptiles, though more complex than the alveolar structure of the Ophidian lung. The corresponding bronchus opens at once into this subcellular lung, the alveol

Fig. 115.

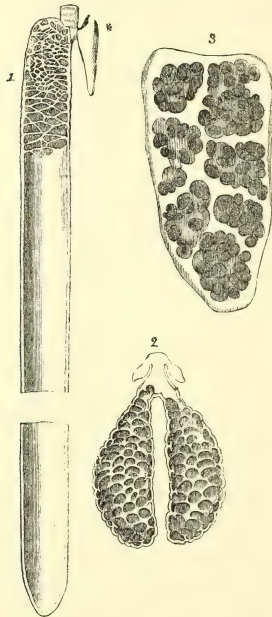


Fig. 115. 1, Lungs of a serpent; the right one only is fully developed; it is of such length, that the upper and lower portions alone are represented; the upper end is trabeculated and sacculated. 2, Lungs of the frog, showing their simple cellular character. 3, Portion of the lung of a turtle, showing its compound cellular structure.

at the upper part of which, are supported by fine cartilaginous trabeculae; it has been aptly compared to a single ultimate lobule of the lung of the Bird; but the layer of capillaries is single, and is exposed to the air on one side only. The respiration of the Amphibia, is comparatively imperfect, and their blood is cold; moreover, it is partly

performed by the surface of their moist skin, as has been proved by their continuing to exhale carbonic acid, after the removal of both lungs, an operation which they, for a time, survive. Even, in temperate climates, the Amphibia hibernate beneath the water; and, in that state, they respire solely by the skin; but in summer, simultaneously with a greater general energy, their respiration becomes more active, and then they breathe by the lungs also. The necessity for respiration, increases in these and in other cold-blooded animals, with the elevation of the temperature of the surrounding medium, which excites them to greater activity of body. In the Siren, and Amphiuma, the interior of the lungs is only slightly alveolar, presenting the last traces of a structure like air-cells; in the Proteus, the lungs are smooth on their internal surface, like the air-sacs of the Fish; the trachea is membranous, and the glottis is a simple cleft.

In the early larval, or tadpole, state, all the Amphibia breathe aquatically, and some species retain the means of so doing, in the adult condition; but all of them then have lungs, however simple.

To *Fishes*, the aquatic form of respiration is proper; but, as the homologue of the lungs of the other Vertebrata, the *air-bladder* of certain species requires mention. The air-bladder of the Fish, is a simple membranous sac or bag, placed beneath the spine, sometimes elongated, cylindrical, or fusiform, sometimes pyriform, sometimes provided with simple diverticula, more rarely with short branched tubuli; sometimes it is double, one part being longer than the other, thus resembling the asymmetrical lung of the Serpents. The air-bladder always contains some air. It is usually a closed sac; but, in many cases, as in the pike, carp, salmon, and herring, it communicates, by means of a short open duct, the *ductus pneumaticus*, with the œsophagus, near the stomach or higher up; in the *Lepidosiren*, it communicates with the pharynx, and even opens into it by a slit like a glottis; it is also bifid, and slightly alveolar, closely resembling, therefore, a simple saccular lung; it sometimes presents vascular projections in its interior. The idea, that the air-bladder is the homologue of the lungs, is supported by the fact, that in the embryos of the so-called pulmonated Vertebrata, the primitive lungs originate as little buds developed from the sides of the upper part of the œsophagus, which afterwards become hollowed out and branched. There is no homology between the gills and lungs in the Vertebrate series of animals; they have analogous functions, but they are totally distinct parts of the organism.

Certain fishes, as the Loach, can swallow air which probably enters the air-bladder; but, in other cases, and especially when this organ forms a closed sac, air must be alternately excreted from the blood and absorbed by it, according as the bladder is full or empty. In the *Amphioxus*, the alimentary canal aids in the respiratory process. The analysis of the air in the air-bladder, sometimes shows a large proportion of carbonic acid, and sometimes little more than nitrogen. In a few species, in which it is of great size, and communicates freely with the pharynx, the air-bladder may be regarded as a feeble sub-respiratory organ. In the great majority of cases, however, it is a rudimentary art, exercising little or no respiratory function; it is large in the flying fishes, and in some others capable of energetic and sustained exertion. As elsewhere mentioned (vol. i. p. 232), when distended, it

diminishes the specific gravity of a Fish supported in water, and also alters the centre of gravity of the animal. It is usually absent in what are called ground-fishes, which live in deep water; but its presence or absence appears to follow no precise rule, either as regards the habits, size, or generic position of the Fishes in which it exists or is wanting.

Mollusca.—The Pulmogasteropods offer examples of Non-Vertebrate aërial breathers; they are terrestrial in their habits. In the Snails, for example, a large sac communicating with the external air, by an aperture situated on the left side of the neck, is found in the shelled varieties, beneath the back part of the mantle, in that portion of the body which occupies the smaller coils of the shell. It has numerous blood-vessels ramifying upon its walls, and is usually lined with cilia. This simple sac may be taken to represent the primitive idea of a lung, that is to say, a sac, formed by an inversion of the surface of the body, lined by a thin moist membrane, communicating with the air, and possessing distributed upon its walls, bloodvessels, which have thin coats and a constantly moving blood-current in them. Such an organ becomes perfected by increase of size, by multiplication of its parts, so as to constitute a multilobular lung, by subdivision of its internal surface into saccules or air-cells, and by the penetration of air-tubes into its numerous lobules. The remaining Gasteropods, and, indeed, all other Mollusca and Molluscoida, breathe aquatically.

Annulosa.—Numerous instances of air-breathing animals, occur in this Sub-kingdom. Entire Classes without exceptions, such as the Myriapoda, the Arachnida, and the extensive and most important Class of Insect breathe in this way. Of the Annelida, a few only are terrestrial and respire air; these, such as the earth-worms, have pairs of small sacculi opening on the sides of the body, in each segment; but they are usually filled with mucus. Similar structures exist in the leech. The air-breathing Annulosa, generally, however, do not breathe by soft membranous compound sacs like lungs, or by soft air-bladders, or even by simple soft sacculi like those of the land-snails; but they have internal air-chambers surrounded by stiff walls, so that they are kept constantly patent, and are not easily compressed.

In the *Myriapoda*, these chambers are saccular, a pair of symmetric sacs existing in each of the many segments of the body; they communicate by short membranous tubes, the walls of which exhibit spiral lines, with little apertures on the sides of the segments, named *spiracles* or *stigmata*. From these sacs, in one species, forming a step towards the condition of Insects, other short twigs ramify into the body, or large symmetrical lateral trunks connect them all together. In this way, air conveyed into close proximity with the nutrient fluids, and respiratory interchanges are accomplished.

In the *Arachnida*, air-sacs exist in the spiders, communicating immediately with spiracles or stigmata on the surface of the body, and frequently having their internal membrane *plicated*, so as to increase the surface for exposure to air, for the aëration of the fluids of the body. This plicated structure is associated with a more perfect condition of circulation, and compensates for the comparatively limited distribution of the air, in these active and powerful animals. In other Arachnida, air-chambers are tubular, constituting tracheæ, as found in the mites

The *Insects* possess in greatest perfection, this particular modification of an aerial respiratory apparatus, viz. a series of almost incompressible canals or tubes, instead of sacs. In these exceedingly active and energetic animals, most of which are organised for flight, the respiratory apparatus consists, first of tubuli, which commence at the *spiracles* or *stigmata* found on each side of certain segments of the body, and, after a short course, lead into two longitudinal lateral tubes, extending from one end of the animal to the other. From these principal tubes, branches are given off for each segment; these branch again and again, until the finest ramifications penetrate the substance of every organ, especially the muscles, and even the ganglionic nervous centres, and the complex eyes. These tubuli, large and small, constitute the well-known *tracheæ* of Insects. They are recognised under the microscope, by the beautiful structure of their walls, which are composed of coherent spiral fibres arranged in the most regular manner, and maintaining by their elasticity, the whole tracheal system in a patent state, resisting the pressure to which they are subjected during muscular effort. By these open canals, air is freely introduced into every portion of the Insect. In many perfect Insects, especially in those of powerful flight, the body or abdomen is made to perform active movements, by which air is drawn in and out through the spiracles. Closure of the spiracles, or the filling of the tracheæ with oil, speedily asphyxiates these animals. Although, therefore, the circulatory apparatus is limited to a dorsal vessel, with large venous sinuses and interstitial lacunæ, without capillary vessels, yet the respiratory apparatus is diffused through every organ and portion of the body, and the aëration of the blood is most complete. The respiratory function of these, the most perfectly developed examples of the Annulose animals, is, in the majority of species, extremely active, in harmony with their general energy and comparatively high temperature. In the largest insects, and in those which, though of smaller size, possess remarkable powers of sustained flight, as the Bee-tribe, the longitudinal tracheal trunks are dilated in certain segments, so as to form *air-sacs* with rigid walls. The size of these, presents considerable variation, being largest in species possessing the greatest powers of flight. The wings of the perfect Insect have no homology with the true limbs, for they spring from the dorsal and not from the abdominal surface; in their structure and mode of evolution, they are more like respiratory organs, being filled with ramified tracheæ.

The tracheæ and their dilatations in the flying Insects, sometimes designated the Birds of the Non-vertebrate Creation, have been supposed, like the membranous and osseous air-cavities in Birds, to diminish the specific gravity of the body during flight, by the warmer air in them; but any such effect must be immeasurable. Their hollow, stiff structure, however, utilises the material employed in the most admirable manner, and so relatively diminishes weight; whilst the large dilatations or sacs met with, especially in Insects of flight, may serve as store-houses for air, the spiracles being perhaps more or less closed during that act.

Insects absorb, and convert into carbonic acid, a relatively large quantity of oxygen, even during rest; but the respiratory interchanges are much more active during locomotion. A bee will perform during the excitement immediately following its capture, as many as 125 respiratory

movements of its body per minute; but after an hour and a half, these may decline to forty-six per minute. In the first hour of an excited respiration, one-third of a cubic inch of carbonic acid has been found to be generated, a larger quantity than was produced in twenty-fours by a bee in its quiescent state, and far more than is given off by the lungs of a Man, in proportion to his weight (Newport). In the larval condition, as exhibited in caterpillars and grubs, Insects are also provided with stigmata, lateral tubes, and tracheæ; and so is the pupa or chrysalis of those insects, which pass through the perfect stages of metamorphosis. But the respiratory process in the pupa, is less active than in the perfect Insect, and in the chrysalis, less active than in the larva. It is curious that the larvæ of certain insects, as of the gnats and Ephemerae or day-flies, and the dragon-flies, are purely aquatic in their habits; but still for the most part, they also breathe by tracheæ, the spiracles of which exist only in the hinder portion of the animal; these they protrude above the surface of the water, for respiratory purposes. In the larva of the gnat, one of the spiracles of the tail segment, is provided with a tubular prolongation, the mouth of which, beset with fine setæ which retain vesicles of air, is made to reach the surface of the water, so that the creature can breathe whilst the rest of the body is submerged, and the head turned downwards, in order to watch for its prey. The larvæ of the Ephemerae, still more curiously, breathe by external tuft-like or leaf-like thoracic or abdominal gills, connected with the tracheæ or by similar organs situated in the intestinal canal; but in the perfect state, like other Insects, they breathe by tracheæ. Aquatic beetles come to the surface to breathe, or carry globules of air below the water. The same habit prevails among certain Arachnida, some of the water-spiders even building nests beneath the water, and carrying down air to them, which they can afterwards respire.

Aquatic Respiration.

In this form of breathing, the physical process concerned, is simply that of the *moist or false diffusion of gases* in a state of solution, those of the blood or nutritive fluids of the animal interchanging with those of the water, which, whether fresh, brackish, or marine, is the universal medium of aquatic respiration. That water contains air, is shown by placing it under the air-pump, or by boiling it, which processes abstract or expel the air, and render it unfit to support aquatic animal life. The quantity of free oxygen contained in water, is, of course, much less volume for volume, than it is in air, inasmuch as the source of the oxygen, is the air itself, held in solution. But the air, dissolved in water, is somewhat richer in oxygen than the ordinary atmosphere; this is explained by the fact that oxygen is twice as soluble as nitrogen in that fluid. Nevertheless, the gaseous interchanges in aquatic respiration, are necessarily slower and less energetic than in aerial breathing. The temperature of aquatic breathers is low: they maintain a heat very little raised above that of the surrounding medium, which is also a much better conductor of heat than air, and so robs them quickly of the caloric; their movements and other vital acts, are comparatively sluggish and slight; their life is more vegetative, and even those which have perfect circulation, are characterised by possessing cold blood. The

Mammalian aquatic species, such as seals, porpoises, and whales, though chiefly or entirely inhabiting the water, are yet air-breathing animals provided with lungs, and warm-blooded.

In water-breathing animals, in which a distinct circulation of blood exists, a special respiratory organ is always present, connected with the circulatory apparatus. With the exception of Insects, this is true likewise of air-breathing animals. The more perfect the circulation, the more carefully must respiration be provided for; otherwise, carbonic acid, accumulating in the blood, would be speedily conveyed to the nervous centres, and produce rapid poisoning. Such an event is more imminent in the warm-blooded air-breathing, than in the cold-blooded water-breathing animals.

The most perfect breathing apparatus, for *aquatic* respiration, consists of exceedingly vascular projecting membranous processes of various forms and complexity. In the lower animals, such processes are more simple, and in the absence of a distinct circulation, they are ciliated upon their surface. These projections are named *branchiæ* or *gills*; they differ in structure, as much as the lungs of the air-breathing animals. Again, in certain forms of aquatic animals, and in some Protozoa, there are found, with or without gill-like projecting organs, remarkable internal ramified tubes or vessels, communicating, by an opening, with the surface of the body, and partially ciliated in their interior; these are the so-called *water-vessels* or water-vascular system; they appear to have a respiratory office. In still lower aquatic animals, destitute altogether of vessels, certain hollow ciliated portions of the surface, or interior, of the body, exist, named *ciliated sacs*; in others, *ciliated tubes* are present; often the cilia are methodically arranged on the surface, or in the interior of the body; lastly, in the lowest forms, these microscopic moving organs cover a portion or every part of the minute organism, and so are auxiliary to respiration.

Vertebrata.—The highest of this Class which have gills, are the *Amphibia*. In the larval or tadpole condition, all these animals have minute gills, and frequently even two sets of these organs. The first set are called the *external gills*, and consist of soft processes slightly branched, or very much subdivided, or even plumose; they are attached to the side of the neck and project freely into the water. In the larva of the higher or tail-less Amphibia, the frogs and toads, the external gills remain only for a few days; but in the tailed salamanders or newts, they exist for a longer period, and in the lowest Amphibia, they persist throughout life. They are, at least when newly developed, always covered with cilia, and each minute subdivision or branch contains a looped capillary vessel, one side of which conveys outwards, the de-oxygenated venous blood, and the other inwards, the oxygenated or arterial blood. The second set of gills, found in certain Amphibia only, are named the *internal gills*; these appear in frogs and toads after the casting of the external gills; they consist of minute fringes of vascular processes attached to the cartilaginous branchial arches of the hyoid apparatus, and are protected by a fold of the skin of the neck, so as to lie in a sort of *branchial chamber*, which communicates with the pharynx; the opening on the right side of the neck, very early becomes closed. Water reaches these internal gills, by flowing in through the mouth or nose, and then out through a small orifice on the left side of the neck, the movement

of the water being caused by an act resembling that of deglutition. It is these internal gills, found in some of the Amphibia, which are the representatives or homologues of the gills of Fishes; they are not developed in Menobranchus and Amphiuma. In the frogs, toads, and true salamanders, both sets of gills disappear; hence these are named *Caduceibranchiate* Amphibia; they afterwards breathe by the lungs and skin only. In the salamandroid *Perennibranchiate* Amphibia, including the Axolotl, Menobranchus, Siren and Proteus, the gills are persistent; they are really the external gills, though they may become attached, as in the Axolotl, to the first branchial arch of the hyoid apparatus.

In *Fishes*, the branchiæ or gills, which are always internal or covered, attain their highest development and most complex forms. They usually consist of numerous comb-like processes, supported, like single or double fringes, on the branchial arches of the hyoid apparatus, and forming four or five laminæ on each side of the pharynx. They are, in some cases, as in the Cartilaginous Fishes, concealed by the integuments; but in others, as in the Osseous Fishes, by a moveable osseous and cutaneous covering, named the *operculum*. In the latter case, only *one external gill opening* exists on each side, the operculum overlapping all the branchial arches; but internally the gill-chamber opens into the pharynx, by separate clefts or apertures between the branchial arches. In the former case, however, the gill chamber is completely divided into passages, varying from *three to seven* in number, each having a separate internal and external aperture, corresponding with the clefts or spaces between the branchial arches. In some of the lowest forms, the gills are mere folds of membrane, lining distinct sacs. In the Myxine, the branchial outlets unite into a single canal, which runs backwards, and opens on the under surface of the fish, at a sort of abdominal pore.

The extent of surface obtained by the comb-like fringes of the gills of Fishes for exposure to water, is very large, especially in the rays and skates. The water drawn into the opened mouth, is forced, at intervals, by the hyoid and pharyngeal muscles, between and over the gills, in the direction of their fringes, and is rapidly expelled at the sides of the neck, the action, as seen in an ordinary fish, being accompanied by regular movements of deglutition, and by a characteristic opening and shutting of the opercula. In the Cartilaginous Fishes, the water passes in streams from the lateral openings, which are sometimes more or less valved. Drawing a fish rapidly backwards in the water, may asphyxiate it, by bending up the branchial fringes, if the opercula be open, or by exclusion of water, if these be closed. Each fringe-like process of a gill-plate, is supplied by a branch of the *branchial artery*, which brings dark or venous blood from the heart and bulbus arteriosus; this divides into minute vessels, which end in the *branchial capillaries*; from these again, the *branchial veins* arise, which pass back to the base of the gill, and all combine to form the aorta. In passing through the gills, the blood is oxygenated. As the heart of the Fish is branchial, all the blood returned from the body is propelled through the gills, before it is again distributed to the body; nevertheless the respiration of fishes, being aquatic, is feeble, and their temperature is cold. The gills of fishes, are not ciliated on their surface but it is necessary that they should continue moist, or the usual respiratory interchanges between the blood, and the air dissolved in the water

would soon cease. Respiration will, however, go on for a short time in the air, provided that the gills remain moist. Certain fishes, as the eel and others, leave the water for a time. The Anabas of Ceylon, is said even to climb up trees and bushes after food; on the sides of its head, just above the gills, the pharyngeal bones are convoluted, and the anterior branchial arches support chambers with laminated walls, for holding quantities of water. Fishes are necessarily suffocated when removed from the water, the gills becoming first clogged and then dry, circulation and respiration in them being both arrested. They are also asphyxiated in water, which no longer contains oxygen in solution, or even when foreign substances are dissolved in it; sugar speedily destroys them. In that exceptionally organised marine animal, the Amphioxus, the mouth is provided with ciliated *lobes*, which, by ciliary action, propel the water into the pharynx. This cavity is dilated, has its sides supported by a complex lattice work of branchial cartilages, upon which the branchial vessels are placed; its sides are perforated by numerous slits, upwards of 100 in number, the edges of which are ciliated, and which lead into the perivisceral cavity of the abdomen. The water used for respiratory purposes, is expelled from this cavity, by an opening named the *abdominal pore*. Moreover, the entire alimentary canal is ciliated internally, and the water which passes through it, may also be employed in the aëration of the blood.

On comparing the entire series of the Vertebrata, as regards their mode of respiration, it is seen, that in the adult state, the Mammalia, Birds, Reptiles, and Caducibranchiate Amphibia breathe by lungs; that the Perennibranchiate Amphibia and the tadpoles of the Caducibranchiate kinds, breathe both by lungs and gills; and lastly, if we disregard the sub-respiratory air-bladder occasionally present, that Fishes breathe entirely by gills. The respiratory process in these animals, is, however, much more active than in the aquatic Non-vertebrata, which we have next to describe. This is due to the comparatively greater size of the gills, to their more perfect and complex structure, to the special contrivances for moving the water over their surfaces, and to the proximity of the heart to these organs.

Mollusca.—Of these chiefly aquatic animals, the most highly developed gills exist in the highest Class, the Cephalopods, in which the branchiæ, being very large but non-ciliated, consist of foliated laminæ, united by a common stem, which supports the branches of the branchial arteries and veins. The gills are lodged, one or two on each side, in the cavity of the non-ciliated mantle, which has two orifices, one by the side of the neck, at which the water enters, and another placed at the extremity of the tubular process called the funnel, from which the water passes out. The movement of the water is accomplished by the alternate dilatation and contraction of the muscular walls of the mantle. In the Pteropods, the branchiæ are also laminated, being placed sometimes within, and sometimes without, the mantle, and being always ciliated. In the naked species of Branchio-gasteropods, the gills consist of ciliated, fringed, sometimes tubular processes, projecting into the water (Nudibranchiata), and arranged either along the sides of the body in tufts (Tritonia), or else in a circular disc-like manner on the dorsal region (Dorsibranchiata), or around the lower opening of the alimentary canal (Doris); sometimes a fold of the mantle partially or completely covers them. In

those kinds which have univalved shells, the gills consist of ciliated plicated fringes, lodged in the last spire of the shell, the water gaining access to the cavity in which they are contained, sometimes by a long tube, and sometimes by a wide opening. Amongst the lowest Branchio-gasteropods, are some species allied to the Nudibranchiate group, which have no branchiæ, but are believed to respire by means of their surface only, or by that, aided by certain ciliated extensions of the digestive cavity. A few genera, such as *Onchidium*, possess, besides arborescent branchiæ, distinct air-sacs, showing a transition between the branchiate and pulmonate divisions of the Gasteropoda. In the bivalved Lammellibranchiata, mussels, oysters, and others, the gills consist, as their name implies, of two pairs of flat laminae, composed of a double layer of membranous rods, covered with fine cilia, and supporting the bloodvessels. In some genera, these branchiæ are freely exposed, when the valves of the shell are open (oyster); in others, they are enclosed by the ciliated lobes of the mantle, at each end of which, an aperture exists for the entrance and exit of the water, which is driven through, by ciliary action.

Molluscoida.—Amongst these, which are all aquatic, the *Ascidioda* possess, in the anterior part of the body, large *respiratory atria* or *chambers*, or branchial sacs, lined with cilia, and communicating with the exterior. These atria are formed by an expansion of the part formerly named the pharynx, which is supported by a rod, called the *endostyle*, the sides of which are, in some species, cleft by numerous slits, through which water passes into an interval between the branchial atrium and the proper walls of the body, and then escapes at the opening of the mantle. In the *Brachiopoda*, the cavity of the mantle itself, is the chief respiratory chamber; it presents vesicular dilatations covered with vessels, which probably act as gills. In the *Polyzoa*, the perivisceral cavity, which contains nutrient fluid, is prolonged into the numerous, delicate, tentacular processes, arranged around the oral aperture, which are covered with rows of beautiful cilia; hence the fluid in their interior, is aerated by the currents of water on their surface.

Annulosa.—The aquatic *Annulosa* are represented only by the *Crustaceans*, and the *Tardigrade Arachnida*. In the larger *Crustacea*, the gills or branchiæ present the form of flattened laminae, which, in the higher forms, such as the lobsters and crabs, are enclosed in proper branchial cavities within the shell; in the lobster, there are twenty-two branchiæ on each side. Through these cavities, copious streams of water are propelled by the continual movements of special flapping organs, consisting of the last joints of some, or all, of the abdominal limbs, which are flattened out for that purpose.

In the land crabs, which are drowned if kept in water, but which remain on land a long time, the gills are moistened by the watery contents or secretion of a spongy or laminated organ, situated, with the gills, in the gill-chamber. In still lower and smaller *Crustacea*, the branchiæ consist of delicate foliaceous or flabellar organs, attached to the under side of the segments of the body, which project into the water, and are usually kept in a constant state of motion. In the *Crustacean Onisci* or woodlice, and allied forms, which inhabit moist places, there exist near the covered gills, networks of air-tubes, or even air-sacs, thus approaching the *Insects*. In some of the lowest aquatic *Arachnida*, as the *Pycnogo-*

ida, no special respiratory organs have been detected. No cilia exist in any of the aquatic Arthropodous Annulosa. It has already been mentioned, that the larvæ of certain Insects, which live in water, breathe by gill-like appendages connected with the abdomen, or with the intestinal canal. The *Annelida* or worms are generally branchiated; the gills are composed of a highly-divided delicate membrane, either branched or tufted, and usually ciliated; they are sometimes external and situated either on the back, on every segment of the body, as in *Nereis* and *Eunice*, or around the head only, as in *Serpula*; sometimes they are internal or covered, as in *Polynoe*; or they are represented merely by ciliated sacs, as in the leech.

Annuloida.—These are, also, either aquatic, or parasitic in the interior of other animals. Such as have soft integuments, probably respire through the skin. None ever possess branchiæ; but special provisions for the respiratory function are met with. Thus, in all the worm-shaped *Scolecida*, there exist peculiar ramified contractile vessels, the trunks of which open on the surface of the body, and are in part ciliated in their interior; these are the so-called *water-vessels*, which are supposed to be subservient to the respiratory process. In the Rotiferous animals, ciliated discs of the most varied shape, perform this function. In the Echinodermata, respiration seems also to be performed, partly by the sides of the perivisceral cavity which communicates generally with the exterior, admits the sea-water, and is lined with cilia; and partly by the contractile ambulacral vessels, which can also be distended with fluid. In the Holothurida, the perivisceral cavity is closed; the ambulacral system is reduced to its lowest condition, but important ramified tubular organs, communicating by a trunk with the cloaca, and projecting into the perivisceral cavity, are regarded as respiratory organs; they are contractile and are lined with cilia.

Cœlenterata.—All of these are aquatic. They possess no distinct circulatory organs, and accordingly no separate respiratory apparatus; respiration seems to be accomplished by the interchange of oxygen and carbonic acid, indifferently through any part of the external surface, or specially perhaps at certain ciliated portions of the internal surface of their body cavities, and within the numerous ciliated tubular prolongations of that cavity, which ramify in the soft disc of some of those animals.

Protozoa.—These universally aquatic animals, exhibit the same want of distinct respiratory organs, unless the *contractile vesicles* be of this character. In the Infusoria, more or less of the surface of the body is ciliated. In the Sponges, the tubular passages through the body, form respiratory surfaces, being in many species provided, at certain points, with cilia. Lastly, in the Rhizopods, or Foraminifera, and in the still humbler Gregarinida, not even cilia are present; but the almost structureless or simple cell-like body of these animals, must be stimulated, disintegrated and purified, by direct absorption of oxygen, and exhalation of carbonic acid, so far as is necessary for their simple life.

The presence of *vibratile cilia*, on the respiratory surfaces of the lower forms of most aquatic animals, is a noticeable anatomical fact; they often occur in the embryonic, if not in the adult condition. They serve, when present, to change continually the stratum of water in immediate contact with the breathing surfaces; and, according to some, their motion is even to be attributed to the active chemical changes

which take place on those surfaces. They are not, however, essential, for they are not always present. Their absence from the branchiæ of the Cephalopods amongst Mollusca, and of the Crustacea, amongst Annulosa, form the most striking exceptions. Amongst the aquatic Vertebrata, they are not found on the gills of fishes, unless upon the branchial apparatus of the singular Amphioxus; they exist on the temporary gills of the Amphibia, but probably not on the permanent gills of the Perenni-branchiate forms. Amongst air-breathing animals, they are wholly absent in the sacs or tracheæ of the higher Annulosa. In the lowest air-breathing Vertebrata, viz. the Amphibia, they exist in the lungs as well as in the respiratory passages; but, in all other instances, they appear to be confined to the air-passages and air-tubes, not extending to the air-cells. It must also be remembered that they are found on other organs, besides those concerned in respiration.

ANIMAL HEAT, LIGHT, AND ELECTRICITY.

ANIMAL HEAT.

Inorganic bodies have a constant tendency, by losing or gaining heat, to adapt themselves to the temperature of surrounding media or objects. They may also be artificially cooled, or artificially heated, to all possible degrees. The same is true of dead organised bodies, within the limits of combustion, as of a dead tree, or of a dead human body. Living plants and animals also receive, or give off, heat physically, but they have, besides, a common power of resisting external temperatures; with plants, this power is very feeble, but with animals it is more marked. In the higher animals especially, there is an inherent power of maintaining a temperature differing from that of the surrounding media, which are in general cooler, but may be warmer, than their own bodies. Moreover, each kind of animal is able to maintain, within a certain range, a temperature proper to itself; but, since even living animals, like dead ones and inorganic bodies, exhibit the same physical phenomena of absorption, conduction, and radiation of heat, they undergo constant changes, usually in the direction of a loss of heat. Hence, there must exist within them, a power of constant renewal, or production, of fresh heat. The standard temperature of an animal is understood to express its proper heat; whilst the form of heat produced in its body, for the maintenance of this temperature, is known as *Animal Heat*.

This function of producing heat, is universal in the Animal Kingdom, and all the processes of animal life are influenced by it.

Animals have been divided, according to their temperature, into the *Cold-blooded* and the *Warm-blooded* animals, the former being understood to include all the Non-vertebrate animals, and, amongst the Vertebrata, the Fishes, Amphibia, and Reptiles; whilst the Warm-blooded animals consist of the Birds and Mammalia, including Man. Amongst the Non-vertebrate Classes, the Protozoa and Cœlenterata, having no proper blood system, can hardly be designated cold-blooded; yet they have a close relationship, as regards the phenomena of temperature, with that division of animals. It has been proposed to name the Cold-blooded animals, *animals of variable temperature*, and the Warm-blooded creatures, *animals of constant temperature*; because the former have their actual temperature greatly influenced by, that is to say, elevated or lowered, according to corresponding changes in the temperature of the media in which they live; whilst, on the other hand, the latter exhibit nearly a uniform temperature, under important alterations in that of the surrounding media (Bergmann).

In regard to the Protozoa, it has been shown, that when water containing Infusoria, is frozen, these minute creatures are not always necessarily destroyed by being likewise frozen, but each survives for a certain time, surrounded by a little uncongealed watery space; this can only be accounted for, on the supposition that the animalcule continues to produce a minute quantity of proper or individual heat. In the aquatic Non-vertebrate animals generally, a similar power of resisting cold exists; though there are but few observations on the heat-producing powers of these animals. The temperature of a number of earth worms, leeches, slugs, or snails, collected in heaps, has been found to be from $1\frac{1}{2}^{\circ}$ to 2° higher than the air. In the air-breathing Insects, the heat evolved in the larval or caterpillar stage, is sufficient to maintain the body from $\frac{1}{2}^{\circ}$ to 2° in the Lepidoptera, and from 2° to 4° in the Hymenoptera, above that of the surrounding medium. In the chrysalis stage, the temperature is nearly that of the surrounding medium, very little heat being evolved. In the perfect Insect, the temperature may vary in the bee from 3° to 10° , and in the butterflies from 5° to 9° , above that of the air. The temperature of bees, in numbers, as in a hive, may be as high as 16° above that of the air. The nursing bees sometimes reach a temperature of $22\frac{1}{2}^{\circ}$ above that of the atmosphere. Insects, therefore, under certain circumstances possess a heat-producing power nearly equal to that of the warm-blooded animals. The temperature of bees is raised by exercise and excitement, and diminished by rest, sleep, hibernation, and want of food.

In Fishes, the temperature of the blood, is usually from $\frac{1}{2}^{\circ}$ to 1° warmer than the surrounding water at mean temperatures. In other instances, it is 2° to 3° higher, and in a few exceptional cases, in which the muscles and the blood are darker, the heart is larger, and the gills provided with enormous nerves, as in the tunny and bonito, the temperature is still higher; that of the bonito has been found to be 99° , or $18\frac{1}{2}^{\circ}$ above the temperature of the sea (Davy). In the frog, when the external medium has a temperature of about 60° , the animal is from $\frac{3}{5}^{\circ}$ to $1\frac{1}{3}^{\circ}$ warmer than it; but when the external temperature is lowered to about 43° , then the animal is from 2° to $3\frac{1}{2}^{\circ}$ warmer.

The edible frog, enclosed in ice at 21° , has exhibited a temperature of $37\frac{1}{2}^{\circ}$.

In Reptiles, the temperature of the body is still higher, though yet it is dependent on the external temperature. The turtles produce less heat than the serpents, crocodiles, and lizards; the temperature of some of the latter has been found to be 86° , that is, 15° higher than that of the surrounding air. These facts show that in the cold-blooded animals, the temperature is greatly dependent on, and regulated by, that of the surrounding medium, but also that there is a moderate individual heat-producing power even in them. This power, moreover, absolutely increases, like the functions of the animal generally, at still higher temperatures; but yet not so as to enable the animal to reach that temperature.

In the *Warm-blooded* animals, the temperature is high and constant, and, as already mentioned, is, within certain limits, plainly independent of the external temperature, owing to special powers exercised within their bodies. Amongst the Mammalia, the average temperature of the body, is lower than that of Birds, which present the highest temperature of any animals, although their general organisation places them in a lower rank than the Mammals. The ordinary range in the Mammalia, is from 97° to 104° ; in Birds, it varies from 100° to 108° , or even 111° . In the sheep, the temperature has been found to be from 103° to 105° ; in the pig, 106° ; but in the arctic fox, it has been found to be 107° , the air being only 14° . In sea-birds, as in the gulls, the temperature is lower than in other birds, varying from 100° to 105° ; in the common fowl it ranges from 107° to 110° , according to the climate and season, and in the swallow, it is even $111\frac{1}{4}^{\circ}$ (J. Davy).

The temperature of the tissues of the *human body*, speaking generally, ranges between 98° and 100° ; but that of the blood, which is the hottest part of the organism, ranges from 100° to 102° . The blood varies in temperature in different parts, being hottest in the hepatic veins, which bring the blood from the liver; this blood is somewhat warmer than that of the *vena portæ*, and even 1° higher than the blood of the aorta (Bernard). Directly opposite statements have been made as to the temperature of the blood, before, and after, it has passed through the lungs; but the most recent researches favour the conclusion that the blood in the left side of the heart, is nearly $\frac{1}{5}^{\circ}$ lower than in the right side of that organ; a slight cooling process is supposed to occur in the lungs from the air admitted into them. The blood of the superficial veins of the limbs, coming from the exposed skin is naturally cooler, from the influence of the atmosphere, than that of the arteries, which lie deeper; the temperature of the blood in the deep veins, as in the femoral vein, is also said to be about 1° cooler than that in the femoral artery (Becquerel and Breschet). The relative warmth of the organs and tissues, always less than that of the

blood, depends on their vascularity, their distance from the central part of the body, or their proximity to the surface, and on the degree to which they are protected by external covering. Thus, whilst the temperature in the abdomen (in the bladder), has been found to be nearly 102° , even higher than that of the thorax, the temperature under the tongue is about 98° ; and in the axilla 96° ; that of the hands and feet may ordinarily be from 9° to 12° cooler than the central parts, *i.e.* from 90° to 93° .

Various conditions modify the temperature of the human body; neither *age* nor *sex* produce any remarkable difference. The temperature of infants and of old persons, is about normal, so long as they are placed under favourable conditions of protection. But the power of infants and very young children, as well as of the aged, to resist the lowering effects of cold, is less than in the adult. Experiments on the young of Mammalia and Birds, show this; their small bodies, and also those of the human infant, will cool comparatively more rapidly by radiation and conduction, than those of adult animals and Man; their calorific power may be as great, but they cool more quickly. Hence the greater necessity for the protection of clothing, and for artificial warmth.

The influence of *race* is also slight or ineffective. In hot climates, and in hot seasons, the mean temperature of the body is somewhat higher than in cold climates and seasons, the difference being more marked in animals than in Man. The difference, however, usually amounts to not more than from 1° to 2° , showing how slight is the influence of climate, and proving the independence of the temperature of warm-blooded creatures of external changes. According to Dr. L. Davy, however, in a long series of observations, whilst the external temperature varied as much as 22° Fahr., *i.e.* from 60° to 82° , that of the body fluctuated 5.5° Fahr., *i.e.* from 96.5 to 102° . The power of Man to resist, and accommodate himself to, climatic variations of temperature, is greatly aided by shelter, clothes, &c., means of cooling the air, and peculiar selection of food; he can create an artificial climate, and protect himself against its hostile influences. *Sleep* lowers the temperature of the body from 1° to 2° , all the organic functions, even circulation and respiration, being at that time likewise less active. No constant diurnal variations of the temperature of the body, in Man, have been observed; but, in Birds, the highest temperature seems to be attained at noon, and the lowest about midnight (Chossat). *Exercise* increases not only the sensation of warmth in the

body, but actually raises the average temperature; the effects however, being by far most evident in the extremities. Thus the general temperature after quick running, may become nearly 2° warmer; after walking, the deep-seated parts show little or no change, whilst the feet and hands are raised many degrees, the action of the heart and lungs being quickened, as well as that of the muscular system generally, so that more rapid metamorphoses take place (pp. 425, 465). Deficient food and positive abstinence, lower the temperature, why, will be explained hereafter; on the other hand, abundance of food and the use of stimulants, ultimately increase it; but the immediate effect of a meal, or of taking wine, is said to be temporarily to lower the animal heat. The depression of the temperature, observed in animals, in which the skin is covered with an impermeable varnish, has already been mentioned (p. 401). According to Becquerel and Breschet, in rabbits so treated, the temperature falls speedily from 100° to about 75° before death takes place. The change in the colour of the fur or feathers, to white as winter approaches, in the case of Arctic mammalia and birds, retards radiation, and so conserves the animal heat. In *disease*, the temperature of the human body has been found to rise or fall many degrees above, or below the normal temperature. Thus, in fevers with acceleration of the pulse and respiration, in active phthisis, in pyæmia, and in other diseases, temperatures of 104° , 106° , and $108\frac{1}{2}^{\circ}$, have been noted, and in tetanus of $110\frac{3}{4}^{\circ}$, *i.e.* nearly 10° higher than the normal standard. On the other hand, in asthma and cyanosis, or the so-called blue disease, in which, owing to communication between the right and left auricles of the heart, the blood is imperfectly oxygenated in the lungs, the temperature of the body is unnaturally low; this is also the case in syncope, apparent death, and cholera, in which last disease, the blood becomes so thickened as scarcely to circulate. In the stage of collapse in cholera, the temperature of the surface of the body may be, according to different authorities, as low as from 80° to 67° , *i.e.* from 15° to 28° below the ordinary temperature of the exposed skin. The sensation of heat, or the opposite one of cold, experienced by a person in disease, does not always correspond with the actual temperature of the body; for in the cold stage of ague, though the feeling of cold is extreme, the temperature of the body may be actually raised (vol. i. p. 470). On the approach of *death*, generally, with a feeble pulse and respiratory action, combined frequently with

the evaporation of profuse perspiration, the temperature is gradually lowered : first, in the hands and feet, then in the forehead, ears and nose, and afterwards in the parts nearer to the centre of the body. It has been observed, not only in cholera, in which the temperature of the body is lowered from the disease during life, but also in yellow fever, in which the body is hotter than natural, that the temperature after death undergoes an actual elevation ; this is probably to be accounted for, by the conduction of heat from the central parts, together with the cessation of the cooling influence of the evaporation and the cutaneous exhalation.

After death, the cooling process goes on, in accordance with the physical laws which regulate the temperature of inorganic moist bodies, the rate at which this cooling takes place, depending chiefly on the external temperature and relative motion of the air, on the degree of exposure of the body, its condition of emaciation or obesity,—fat being a bad conductor—and on the conducting power of the clothes, or other objects in immediate contact with the corpse.

Effects of Cold on the Human Body.

The power possessed by the human body, of maintaining its proper temperature, independently of external conditions, is limited within certain ranges ; conditions of cold or heat are met with, which not only produce great inconvenience, but which, in the absence of special protection, may exercise a fatal influence. It has been shown experimentally, that, when a Mammalian animal has lost about 20° to 21° , or about $\frac{1}{4}$ th of its normal heat, it suffers so greatly, that a further loss of heat is fatal to it, death ensuing from debility or congelation. On the other hand, an addition to the temperature of the body of a Mammiferous animal, of about 13° , is equally serious, constituting a limit beyond which death speedily occurs. Hence in Mammalia generally, an artificial elevation of the temperature of the body, is sooner fatal than an artificial lowering of that temperature. The same is probably true of Man, a greater range of temperature, in disease, having been observed previous to death, in the descending than in the ascending scale of warmth. The relative degrees of external heat and cold, which are endurable by Man, with proper precautions, in the different climates of the world, also prove that he can sustain, without injury, a greater diminution than an elevation of the external

temperature. In the arctic regions, the thermometer has been recorded at temperatures as low as from -55° to -70° , the latter temperature being no less than 170° below the normal temperature of the blood; whilst in the other direction the highest temperature registered in the tropics, is about 130° in the shade, viz. about 30° above the blood heat. Man is much more readily inured to cold than to heat; and the inhabitants of temperate regions, when they remove to the tropics, require to be more specially acclimatised, and can scarcely avoid becoming ill; whilst, in removing to colder latitudes, with due precautions, health may be more easily preserved. Nevertheless cold, to the feeble and aged, is the great enemy of animal life, and the chief remote cause of human mortality.

When the living human body is exposed to the prolonged action of extreme cold, without protection, a gradual benumbing of the sensibility, a lowering of the circulation and respiration and a general torpidity of the system, are produced. These effects occur more readily in children, and in infirm, ill-fed, or starved persons, and also in aged persons; and lastly, in those who are previously overcome by fatigue, or by the narcotic effects of alcohol. The nervous system is specially subjected to the influence of cold; the senses frequently act irregularly giving rise to noises in the ears, and spectral visions; delirium often supervenes, and, finally, an irresistible tendency to, and desire for sleep, takes complete possession of the frame. Further exposure to cold, then produces a fatal coma. Isolated examples of death from this cause, happen in the experience of civilised life; but large numbers of troops, and even entire armies, especially when ill-fed, clad, and protected, have been lost from the injurious effects of extreme cold. The effect of cold is most marked, when the body itself is motionless. Its evil fatal effects occur more rapidly, however, when the atmosphere itself is in motion; because, then, fresh quantities of cold are brought continually in contact with the body, and conduct away its heat more rapidly. A moist atmosphere is also detrimental, on account of its being a better conductor than dry air.

The *local effects* of extreme cold are usually manifested, first upon parts unprotected by covering, or most distant from the centre of the body, such as the feet, hands, face, or ears, and especially the nose. In such case, the skin first becomes red, from congestion of the dilated small arteries and capillaries; next it becomes blue, from arrest of the circulation; and aft-

ards of a tallowy white, from the extreme constriction of the arteries supplying the part, so that the circulation is first retarded, and then entirely arrested. In perfect congelation, minute particles of ice actually form in the tissues. The ungealed tissues may sometimes be restored to their normal state, provided that the return to a higher temperature, be gradual, as is often and best accomplished, in extreme cases of *frost-bite*, by friction with snow or ice-cold water. By warming the frozen parts too rapidly, the gases of the blood and tissues, set free at the moment of congelation of the water, are expanded in the interior of the capillaries, or amongst the structural elements of the tissues, bursting the former and destroying the latter, and so inducing *gangrene*. In fatal cases of exposure to cold, the body may not, or may, be completely frozen, for the process of congelation of the water in the tissues may penetrate through the whole dead body; but death long precedes such a result, owing, on the one hand, to the fatal benumbing influence of cold on the nervous system, and, on the other, to the retention of some of the proper heat of the body, after actual death.

Effects of Heat on the Human Body.

These are also of great interest. In resisting moderately high temperatures, the problem to be solved, is that of maintaining the temperature of the body, within 2° , or at most 5° , of its ordinary standard, at a time when it is not only producing heat within itself by its vito-chemical actions, but is also, like any other material mass, receiving heat from a surrounding medium, hotter than itself. Thus, the mean daily temperature of the air, in the tropics, during the six summer months, ranges as high as from 80° to 90° , in the shade, the *highest* daily temperature in the shade, varying from 104° to 118° , and the lowest nocturnal temperature ranging from 60° to 66° , the heat thus exhibiting a variation of from 44° to 52° in the course of 12 hours. In exceptional seasons, the highest temperature rises to 130° . Again, in the direct rays of the sun, the heat is, of course, still greater. The effect on the system, is aggravated by motion of the hot air. The adaptability of Man to extremes of temperature, enables him, however, to live in such a climate.

The chief means of maintaining the normal temperature of the body, in hot climates, consists in a large increase in the

amount of the water exhaled from the surface of the lungs and of the skin, especially, however, from the latter. The skin becomes bathed with fluid, the evaporation of which, at the high temperature of the surface and of the surrounding air, occasions a loss of heat and a reduction in the temperature of the evaporating surface. In this way chiefly, the heat of the body is lowered, and maintained nearly at its normal standard. The effect in reducing the temperature of the body, is greater if the atmosphere be dry as well as warm, and then, also, if it be in motion; these conditions favour cutaneous exhalation and evaporation.

It has been shown, by an ingenious experiment, that the evaporation from the surface of the skin of the living frog subjected to high temperatures, is sufficient to maintain the temperature of the animal at stationary point, after it has reached a certain height; whereas moist mushrooms, subjected simultaneously to the same conditions, soon obey the temperature of the surrounding air. The frog and the mushrooms were placed in a chamber filled with dry air, heated from 122° to 140° ; at the end of a quarter of an hour, both the frog and the mushrooms were nearly at an equal temperature, viz. from 62° to 72° each having, by simultaneous evaporation into the hot air, maintained a comparative coolness. As the experiment proceeded, the temperature of both rose to about 100° , at which point, the frog's temperature remained stationary, whilst that of the fungi, no longer able to undergo further evaporation, continued to rise. The continuous exhalation from the moist skin of the frog, was the only cause which could explain the non-occurrence of a further rise in its temperature (De la Roche and Berger).

The effect of evaporation, in reducing the temperature of the living body, may also be illustrated by the results of experiments made on sponges wetted, and porous vessels filled with *hot* water, and placed in a dry oven, in which the air was still *hotter*; these bodies actually lose heat at first, evidently owing to temporary evaporation.

It has been supposed that the living animal body may possess some special means of resistance to external heat, but of this there is no proof whatever. It may be entirely explained by the effects of evaporation.

Thus, when the surrounding air is warm or hot, especially if it be dry, the evaporation from the skin is increased, and the temperature of the body is lowered; whereas, in cold air, especially if this be also moist, the diminished amount of evaporation, tends so far, to conserve the animal heat. The increased perspiration excited by the great heat of the sun, furnishes, for a certain time, sufficient material for evaporation.

there is a limit, however, to the amount of this excretion, and so to its rapidity of evaporation; for when the surrounding air becomes moist, a check being put to the evaporation, the body is no longer thus defended, and its temperature begins to rise. Thus, in a room, the temperature of which was 260° , and the air dry, it was found possible to remain for 8 minutes, by which time, the body was not much elevated in temperature, although the clothes, and other articles in the room, became very hot (Blagden and Banks). A case is on record of a person remaining 10 minutes in a dry hot air-bath at 284° ; whilst Habert, the so-called fire-king, went into ovens heated from 400° to 600° ; but of course, for a much shorter period. Many workmen employed in foundries or glass works, also withstand very high temperatures, the skin being profusely bathed with perspiration; these men of necessity drink large quantities of acid. When, however, the air is moist as well as hot, the temperature that can be endured is much less; for, in a vapour bath, at a temperature of only 120° , the body rapidly gains heat, as much as 70° in 10 minutes, and a feeling of great and insupportable discomfort is experienced (Berger and Dela Roche). It is said, however, that, from habit, the Finns can withstand, for upwards of half-an-hour, moist air or vapour baths gradually raised to 158° , or even to 167° . Animals surrounded by air heated gradually to 200° , speedily die, their temperature being then raised about 13° above their natural standard (The same Authorities). This seems, accordingly, to be the extreme limit of heat endurable by a warm-blooded animal. Most cold-blooded animals are killed by a temperature of about 75° . In civil life, even in temperate climates, direct exposure to the rays of the sun, is often fatal, producing some profound disturbance of the nervous centres, caused either by congestion of the vessels of the brain, owing to quickening of the circulation, or, as some have supposed, by expansion of the blood, from the heat acting on the contents of the skull, the capacity of which is unchangeable. This *coup de soleil* occurs still more frequently in the tropics, amongst troops on the march, or amongst coolies or slaves working on railways or plantations. At Pekin, during about ten days in July 1743, the thermometer stood at the extreme height of 104° in the shade, and in that period 11,400 people died. Under extreme elevations of temperature, the only safety consists in retiring to the protection of houses, and in reducing the temperature of the atmosphere in them by artificial methods, such as by the use of

large fans or punkahs, wet hangings, and other means. Habit accustoms the Chinese, negroes, and others, to bear a greater heat than the natives of temperate climates can support.

Theories of Animal Heat.

Previously to the time of Lavoisier, the heat of the body was more or less vaguely referred to friction, the organic processes of nutrition, the influence of nervous action, and generally to what was understood as the action of the so-called vital force.

In consolidating the discoveries of his predecessors, in regard to the chemical nature of carbonic acid, oxygen, and nitrogen, and in explaining therefrom, the chemical processes and products of respiration, Lavoisier propounded, for the first time, a distinct scientific theory of the production of animal heat. This, now known as the *chemical theory of animal heat*, regards this heat as the result of an oxidation or combustion process, affecting the animal frame. Carbon when heated in the presence of oxygen, unites with that gas and forms carbonic acid, and evolves heat. In like manner Lavoisier argued, that the formation of carbonic acid in the blood, as the result of respiration in living animals, must be accompanied by an evolution of heat.

Though Lavoisier was wrong in supposing that this union of oxygen with carbon, takes place in the pulmonary capillaries nevertheless, his chemical theory of respiration is, with certain modifications and extensions, accepted as the true theory of animal heat.

To found this theory of respiration, it was necessary to compare the amount of heat evolved, during the direct combination of a certain quantity of oxygen and carbon outside the body, with the amount of heat given off from a living animal during its consumption of a similar quantity of oxygen. This enquiry was surrounded by many difficulties.

To obtain data for these purposes, Lavoisier made the first step in the science of *calorimetry*, by burning given quantities of carbon and hydrogen, in his so-called *ice calorimeter*. This was a closed metal case with double sides, between which ice was packed; the source of heat to be subjected to experiment, was placed in the interior of the case, and the quantity of heat given off, was estimated by the quantity of ice which was melted. The *water calorimeter* of Cal

umford is constructed on a similar plan, but is filled with distilled water of a known temperature, and measures the quantity of heat given out in the experiment, by the elevation of temperature of a known quantity of water.

In the first accurate experiments on animals, which were made by Dulong and Despretz, a water calorimeter was employed. The animal was placed in a metal chamber, which was surrounded by a given quantity of water enclosed in a still larger vessel; air was conducted to the internal chamber by one tube, whilst a second long spiral tube passing through the water, like the condensing tube of a still, conveyed away the warm air, which, before it escaped, gave up its heat to that fluid. The stream of air was rendered uniform by an apparatus known as an *aspirator*, a large closed vessel filled with water, and connected with the free end of the coiled air-tube, so that on the gradual escape of the water from the aspirator, through a stop-cock, air was drawn through the apparatus at a uniform rate. In the water of the calorimeter self, a moving fan agitated the fluid, so that its temperature was kept uniform during the experiment. Lastly, the air, as altered by the respiration of the animal, or a part of it, the rest then being measured, was analysed, in order to determine the quantity of carbonic acid produced. It was, at that time, erroneously supposed that this corresponded exactly with the quantity of oxygen consumed. Rabbits or dogs were subjected to experiments, varying from an hour and a half to two hours' duration; and the results obtained by Dulong and Despretz, showed that the amount of heat given off, was from $\frac{1}{5}$ to $\frac{1}{4}$ more than the quantity of carbonic acid produced would account for. In subsequent experiments, made by Despretz alone, it was found that from $\frac{1}{4}$ to $\frac{1}{10}$ of the heat was thus unaccounted for.

The excess in the heat actually produced by the animals experimented on, was supposed to be accounted for, by the action of the heart and the muscles, by that of the blood in the vessels, by the disengagement of heat taking place in the conversion of fluid into solid matter in the nutrition of the tissues, and by some possible action of the nerves. It has, indeed, since been shown, that heat is really given out in muscular contraction. Nevertheless, these supposed causes of animal heat are not primary, but secondary, causes. The heat given off in muscular contraction, is itself engendered by oxidation of the blood of a muscle, or in the muscle itself, during the

so-called parenchymatous respiration. The heat produced by mere friction in the body, must have its source in muscular contraction, and this, as we have just said, is due to chemical change or oxidation. The conversion of fluid into solid substance, in the nutrition of the tissues, is, as will be presently explained, an apparent, and not a real, cause of internal heat; and lastly, any influence of the nervous system is indirect, operating only by exciting organic processes, themselves involving oxidation.

The deficiency of heat-producing power in the quantity of carbonic acid given off by the animals experimented upon by Dulong and Despretz, in comparison with the heat which they simultaneously evolved, may be otherwise accounted for. In the first place, these observers did not determine the temperature of the animals, before and after each experiment, which might have shown some *retention* of heat. But other points are of more moment. The modern researches of Favre and Silbermann, prove that the heat evolved by carbon in its combustion, is greater than that estimated by Dulong and Despretz. It is now known, that more oxygen is absorbed in respiration than is returned in the form of carbonic acid, and this oxygen doubtless is also combined in the system, partly with hydrogen, and partly with sulphur and phosphorus, in either case evolving a certain amount of the heat of chemical combination. The hydrogen of the carbohydrates, being already associated with oxygen in the proportions to form water, is not supposed to be able to give out further heat; but some of that contained in the fat and albuminoid bodies must be oxidised in the system, as was first suggested by Barral, though much of the hydrogen of the nitrogenous substances, appears in the urea. The larger part of the heat is, however, due to the oxidation of carbon in the system. The nitrogen is never oxidised, but passes out almost entirely in the form of urea, and supplies no animal heat. Experiments have shown that carbon, in different states of aggregation, yields slightly different quantities of heat in being burnt, wood charcoal giving out more heat than the more compact coke. The combination of carbon and hydrogen, in the animal economy, is not like that which occurs in artificial combustion, simple and *direct*, but complex, and marked by intermediate decompositions, and most varied products. By many, it has been supposed that these conditions might modify, in some way, the quantity of heat evolved; but it seems more probable, that

number of intermediate stages of decomposition, can alter the total quantity of heat given out; and that, according to the degree of oxidation which occurs, the same amount of heat is evolved, whether this be direct and rapid, or complex and slow. Such decompositions in the body, may affect the amount of heat evolved in *particular organs* or parts of the system, as in the liver, kidneys, or the muscles when in action; but they cannot modify the ultimate or *total* heat product. It has even been conjectured that the oxygen of the atmosphere used in respiration, being partly ozonised, might evolve a larger amount of heat than in ordinary combustion; but the same oxygen is employed in both cases.

The idea entertained by Dulong and Despretz, that a balance of heat might be evolved in the conversion of fluid into solid substances during the act of nutrition, has been mentioned as fallacious. If, indeed, new nutrient matter be solidified in the act of deposition, the process of disintegration of tissue, which precedes or accompanies this, implies a precisely similar amount of liquefaction, which would involve a disappearance of heat. In the digestive and secretory processes, too, the numerous acts of liquefaction imply absorption of heat. Bertholet has recently advocated the view, that *molecular* as well as chemical changes in the body, may give rise to heat. The mode in which a particular, complex, organic compound splits up, may influence the amount of heat which it gives off, and, *locally*, this would affect the temperature; but there is a balance in these actions, and the *total* result is that of simple change. Certain processes of *hydration*, or the assumption and *fixation* of *constitutional water*, which are supposed by Bertholet to be constantly occurring in the system, and to be the actual cause of animal heat, may likewise produce *local* evolutions of heat. The formation from starch, of sugar, lactic acid, and oxalic acid, imply successive acts of hydration, and so perhaps also of the changes of albumen into gelatin, glycocoll, creatin, creatinin, and urea. But a certain quantity of oxygen actually disappears in the body, and two of the chief ultimate products of excretion, carbonic acid and water, are *oxidated*, not simply *hydrated*. Urea alone can be considered such a product, being of course imperfectly oxidised. The supposition, that hydration will explain the formation of all the animal heat, overlooks the far larger amount of heat evolved in the ultimate *oxidation* of the carbon and hydrogen, which leave the body as carbonic acid and water; nor does it ex-

plain the higher temperature of those animals which consume a large quantity of carbon and hydrogen in their food.

With regard to the human body, the estimates of Despretz were made on the supposition that a Man, according to his weight, expired seven times as much carbonic acid as the dog experimented on by him. The quantity thus arrived at, was much less than that computed by all subsequent experimenters, being only equivalent to $5\frac{1}{2}$ oz. of carbon in the 24 hours. Other observers have estimated the daily excretion of carbon in the form of carbonic acid, as 8 or 9 oz. The size and weight of these persons, have not been recorded. Vierordt's estimate, in a number of individuals of different heights, ranges from 5 to 8 oz. In men of a mean height of 5 feet $9\frac{3}{4}$ inches, Dr. Edward Smith estimates the quantity at upwards of 7 oz. The calculations hereafter given, for a person 5 feet $6\frac{1}{2}$ inches, yield a quantity somewhat exceeding 6 oz. of carbon per day. These results are obtained by direct experiments on the absolute quantity of carbonic acid expired by animals or Man. Liebig's estimate is still higher: thus, the quantity of carbon in the daily food, being determined on the one hand, and the carbon contained in the urine and intestinal excretions, on the other, the difference, which was taken to represent the amount given off by the lungs and the skin together, amounted to $13\cdot9$ Hessian ounces, or to upwards of 15 oz. av., of which $\frac{1}{2}$ oz. might be exhaled from the skin, and $14\frac{1}{2}$ oz. from the lungs. This large quantity was found in vigorous soldiers, actively exercised in the open air, and supplied with abundant food. In other examples, viz. in prisoners compelled to labour, the quantity was about $11\frac{1}{2}$ oz. av.; whilst in a prison, where no forced labour was practised, it was about $9\frac{1}{4}$ oz. av. Similarly estimated, the carbon expired daily by sailors in the Danish Navy, was found to be about $10\frac{1}{2}$ oz. av. (Scharling). These results, taken generally, so far confirm the chemical theory of animal heat, that they nearly explain the deficiency of $\frac{1}{3}$ or $\frac{1}{4}$ left by the daily combustion of $5\frac{1}{2}$ oz. of carbon, calculated to be eliminated by Despretz; the excess of oxygen absorbed, which unites with hydrogen, and to a small extent with sulphur and phosphorus, may explain the rest.

The chemical theory of the production of animal heat by oxidation, is in harmony with the fact, that increased respiration increases the amount of chemical decomposition in the body, and simultaneously, the amount of heat produced. Thus, all the conditions connected with *age, sex, period of*

ity and season, as well as those relating to *food*, whether in excess or deficiency, or whether absolutely withdrawn, as in starvation, and to *exercise* (pp. 463-9), which increase the activity of the respiration and the amount of carbonic acid given off, raise the temperature of the body; whereas all those which diminish the respiratory actions and their chemical products, lower that temperature. The relations, as to respiration and temperature, in the lower animals, confirm this view. It has been objected, that not only the respiratory action, but all the other functions of the body, are similarly modified under the above-named conditions; and that, therefore, the variations of temperature may be referable to other processes, as well as to the respiratory interchanges. But since no function of the body whatever, whether it be that of sensation, the guidance of motion, motion itself, nutrition,cretion, or any other function, can be performed without concomitant changes in the chemical molecules of the tissues or organs concerned, and as all these changes are but steps or stages towards a more or less complete oxidation, so any production of heat by them, must ultimately be referred to this chemical action. According to any other view, the heat could be produced from nothing, or without that accompanying conversion or change in the condition of force and matter, which we now know is necessary for its production.

The Cold-blooded animals expire but small quantities of carbonic acid, and their respiration is feeble; whilst opposite conditions are noticeable in the Warm-blooded animals. The most active of these latter, give off more carbonic acid, and manifest a higher temperature, the Carnivorous Mammalia being, in both these respects, above the Herbivorous, the smaller quadrupeds above the larger ones, and, as a Class, the Birds above the Mammals. The relative complexity of the pulmonary organs, the extent of the respiratory surface for the exposure of the blood in the capillaries, and the contrivances for the more frequent renewal of air in the air-cells, keep pace with the increase of temperature in the animals themselves. In the hottest animals known, viz. Birds, special peculiarities exist in the air-cells, and the air-cavities in the bones, with which are associated great force of the heart, great rapidity of its action, a high rate of motion of the blood through the capillaries, a large number of red blood corpuscles, a small amount of evaporation from the skin, and a solid condition of the urinary excretion, involving less loss of heat in its pro-

duction than if it were fluid. The urinary products of Birds are, moreover, chiefly composed of urate of ammonia, which contains less oxygen than urea, so that more of that element passes off as carbonic acid (J. Davy).

The importance of the relation between the quantity of the red corpuscles in the blood, and the temperature of the body, is illustrated by the following numbers, which show the quantity of dried solids of the clot, in 1,000 parts of blood, in a series of animals belonging to the several Classes of the Vertebrata. The hen, 157·1; the dog, 123·8; the tortoise, 80; the frog, 69 and the eel, 60 parts in 1,000 (Prevost, Dumas, J. Marshall).

Animal heat being regarded as the result of a process of oxidation, the small amount generated by the Cold-blooded animals, may be supposed to be derived from the metamorphosis of their own tissues or blood. The same may be true as regards the large Carnivorous animals, the active habits of which, in high external temperatures, may furnish sufficient oxidisable material in the metamorphosed blood and muscular and nervous tissues, to maintain the temperature of their bodies; but Carnivorous animals consume also large quantities of fat, proportionate, it may be remarked, to the coldness of the climate in which they live. In warm climates, Man also might thus sustain his temperature; but in colder regions, where the loss of heat from the body is more rapid, Man, like the Herbivora, whose habits are inactive, must rely upon food also as one source of oxidisable material; and like them, upon food containing more carbon and hydrogen, and proportionally less nitrogen. In different persons, and in different seasons and climates, the extent to which carbonaceous and hydrogenous food is relied on, as a source of combustible material, may vary. An elevation of the external temperature, will lessen the amount of oxidised food; whilst the opposite condition increases it. The excess of carbonic acid exhaled in cold seasons, can only be accounted for, by its proceeding from the greater quantity of food then consumed. On these principles may be explained the fact, that no one dietary is economical adapted to all constitutions, occupations, habits, races, seasons or climates; hence the labourer requires a different diet to the sedentary student, and the native of the tropics different food to the Laplander.

influence of the Nervous System in the production of Animal Heat.

This was formerly greatly exaggerated, and was attributed to some direct action of the so-called nervous force. Many researches upon animals, have shown that injuries to the brain, whether by sections, or by the administration of narcotics, are followed by a lowering of the temperature of the body (Brodie, Legallois, Wilson Philip, Hastings, C. Williams, and Bossat).

In paralysis from cerebral disease in Man, the paralysed limbs are usually of lower temperature than the sound limbs, the difference sometimes being as much as 7° . On the other hand, an elevation of temperature in certain regions, may follow local injuries of the nervous system. Thus, when the spinal cord is divided in the middle of the back, in a Warm-blooded animal, the lower half of the body may become warmer, and remain so for some time. In complete paralysis of the lower half of the body, in Man, from injury of the cord, a similar increase of heat has been observed in the groin, viz. 111° (Brodie). Besides these facts, there are many which show, that general depressing causes acting on the nervous system, lower the temperature, whilst excited conditions of that system are accompanied by increased animal heat, for example, exhaustion or fear on the one hand, and strength or passion on the other. In the last instances, the influence of the nervous system is plainly indirect, and must be attributed to a corresponding diminution or increase of the pulse and respiratory acts. The ultimate influence of alcohol, in raising the temperature of the body, may also be partly due to its specific stimulating effect on the nervous system, and through it, on the heart and respiratory organs; but it may also yield a ready fuel or combustible substance, easily absorbed into the system, and easily oxidised in it; these two last-named qualities may account for its great use in cases of exhaustion from fevers. Again, when the sympathetic nerve is divided in the neck of an animal, or its chief cervical ganglion is removed, the temperature of the whole of that side of the face, may rise even as high as 11° above its normal standard; and this may continue for months with increased sensibility, and increased colour from vascular congestion. In such a case, when the distal end of the cut nerve is galvanised, the temperature for a time falls (Bernard).

The elevation of local temperature, is also believed to be an indirect effect, and to depend on an increase in the flow of blood to the part, consequent upon a relaxation of the walls of the smaller arteries, owing to the loss of controlling power on the part of the vasi-motor nerves (vol. i. p. 389). Serious injury or disease of the spinal cord, may act in the same way, because the sympathetic system has connections with, or origins in, it (vol. i. p. 391). The lowering of the temperature after destruction of the brain, which continues in spite of artificial respiration,—not performed too rapidly, so as to cool the animal by that very process (Brodie), but more slowly (Wilson Philip and Williams),—has also been, of late, most frequently attributed to the loss of some indirect influence of the nervous system, over the strictly chemical heat-producing changes in the system, whether of respiration, nutrition, or secretion. Lastly, it has been suggested that heat may be directly produced in the nervous substance itself, owing to the rapid metamorphoses to which it seems liable, in its healthy and active condition, or else to some transformation or passage of its ordinary force or mode of action, into a calorific action producing heat, in the same manner as, in the electric fish, it may be converted into electricity (Carpenter). The nervous substance must be decomposed in all cases in which it is in action, especially during exercise, when it controls the muscular movements; much movement always produces heat. In such instances, and also in psychical acts, the nervous substance is directly oxidated; so that ultimately, the animal heat evolved, is the result of chemical action.

That the nervous system is not essential to the production of heat in living organisms, seems to be shown by the facts, that in many of the lower animals, no traces of a nervous system have yet been discovered, and, that in certain processes of vegetable life, as in the fertilisation of the ovule and in the commencing stages of germination, heat is also evolved. When, however, in animals, that system is present, it is endowed with such power of control over all the functions generally, and exhibits such innate activity, that it determines and excites waste in other tissues, and undergoes waste in its own, thus indirectly or directly contributing to the production of animal heat.

Uses of Animal Heat.

The modes in which the heat of the body, is expended, are several. First, it supplies the constant *loss of heat* from the body, by radiation and conduction to the clothes or other surrounding objects or media, when, as is usual, these are cooler than the body. It also furnishes the heat necessary to *vaporise* the water of the cutaneous and pulmonary exhalations; it warms the air expired from the lungs; it heats the secretions as well as the body itself; and, lastly, it warms the food and drink taken into the body, when these are cooler than the internal organs, and aids in the solution of digestible substances, and in their metamorphosis for the purposes of absorption. Of 100 parts of heat given off by the body, 72·9 are lost by radiation from the surface, 14·5 by evaporation from the skin, 12 by evaporation from the lungs, 3·5 from warming the air used in respiration, and 1·8 by the urine and solid excreta.

As the standard of temperature remains constant within 2° or 3° , between hot and cold seasons, and tropical and arctic climates, the quantity produced in the body, depends on the external temperature, and must be greater in cold climates, in which the loss is greater, than in warm climates. The amount required to be produced, is also modified by the degree of protection of the body, either by shelter or clothing.

Hybernation.

Amongst the most remarkable phenomena presented by animal life, in the temperate and cold regions of the earth, are those which are known under the name of *hybernation*. During the winter season, a few Mammalia retire into burrows or other shelter, and there, either under the influence of the low temperature, or guided by an inherent instinct or an acquired feeling, pass into a condition of torpor much more profound than ordinary sleep. The marmot, dormouse, and hedgehog, are the most familiar examples of this hybernation in the *Mammalia*. It is remarkable that no *Birds* are known to hybernate, the belief once prevalent that swallows retired to the bottom of ponds to hybernate, being erroneous. Amongst *Reptiles*, both serpents and snakes, as well as land-tortoises, hybernate; and in the *Amphibia*, the frogs and newts. Both serpents and frogs have been kept in this condition, by artificial cold, for three years. Hybernation in Fishes, is not known, unless it be compulsory from freezing of the water. Of the *Non-vertebrate* animals, only terrestrial Species are known properly to hybernate, such as the land-snails and slugs amongst the *Mollusca*, and the chrysalides of certain *Insects*, which pass through a winter, before they change into the imago state. Even in the *Protozoa*, examples are met with, of a winter state or condition, in which those animals undergo the process known as

encystation, so called because in it, they surround themselves with a protective *cyst*, in which they remain dormant, until the return of warmth induces peculiar changes in them, for the reproduction of new animals.

The condition of partial hybernation manifested by certain animals, which collect a store of winter food, such as the *beaver* and others, is named *spurious hybernation*. In this state, the circulation and respiration are not so diminished in activity, nor the temperature so reduced, as in true hybernation; for though the animals sleep much, they, from time to time, arouse themselves to take food.

In the true hybernating Warm-blooded animal, not only the nervous and muscular systems are quiescent, but digestion entirely ceases, no food being taken. The circulation is very slow; the respiratory movements are almost, or according to some, completely, arrested; the interchange of oxygen and carbonic acid in the air-passages, can take place by diffusion only; the absorption of oxygen and the evolution of carbonic acid, are very slight, and the animal heat accordingly sinks; so that, without protection from the cold of the winter season, the animal would die. The respiration which continues, is supported by a store of fat, which serves as fuel during the dormant state; when the creature is roused from this condition, by any irritation, by heat, or by great cold, distinct respiratory movements take place, the heart's beats are quickened, and it manifests increased activity. If the animal be aroused by extreme cold, it soon becomes still more torpid, and may even die if the low temperature be long continued. If excited too completely by warmth, it is also apt to die, unless provided with suitable food, and carefully maintained at a moderate temperature. The suspension of animation in Reptiles and Amphibia, is still more complete; but probably even here some vital action goes on. In many instances, in the lower Non-vertebrate animals, it is probable that all the organic processes are, for a time, completely suspended, as, *e.g.* when they are almost frozen, or first dried and then frozen.

In the Animal Kingdom, considered generally, we observe that a high temperature of the body, not only increases the activity of the various functions, but that this very activity produces, in its turn, a demand for increased respiration, and so engenders an increased amount of animal heat. In the case of Cold-blooded animals, also, an elevation of the temperature of their bodies, by external heat, increases their activity and their demand for increased respiration; and, accordingly, it is found that in Reptiles more carbonic acid is given off in high temperatures, a result opposite to that which takes place in Warm-blooded animals, and in Man. The respiration of Warm-blooded and Cold-blooded animals is said also to differ, if not absolutely, at least relatively, in this particular; that it is only in the Warm-blooded creatures, that some portion of the food, when absorbed into the blood, is devoted at once to respiratory purposes, forming, as it were, fuel immediately destined for the production of heat by oxidation, without having previously entered into the tissues; whereas in the Cold-blooded animals, the tissues only, and not the food merely assimilated into the blood, except perhaps in exceptional cases, and then in a far lower degree, are oxidated, and so produce a small amount of animal heat. In the Warm-blooded animals the blood corpuscles are much more numerous, and the quantity of carbonic acid excreted is much greater, than in the Cold-blooded species.

Spontaneous Combustion.

The highest natural temperature attained, in the healthy state, by any animal, is that noticed in the swallow, about 111° ; the highest temperature observed in the healthy human body, is 102° ; and in disease, 111° . Moreover, experiments have shown that an increase of 13° in the temperature of the body of one of the Mammalia, is fatal. It is obvious that the highest of these temperatures, is entirely inadequate to set on fire the animal tissues; it is even insufficient to inflame the vapour of alcohol. It is, therefore, impossible to believe that the body of a drunkard, whose blood and tissues may even be supposed to be saturated with alcohol, or with some of the products of its decomposition, could spontaneously burn; for the temperature of ignition of the tissues, or of such compounds, is much higher.

Of the so-called cases of *spontaneous combustion*, not one has actually been seen to happen. Naturally, no eye-witness is present, but the more or less consumed body is found; and such occurrences usually take place in persons addicted, during their life, to habits of intoxication. The event is rendered marvellous by the supposition of a spontaneous process of combustion. Of the possibility of burning the dead body with due amount of heat, or even of parts of the body before life in the remainder of it, is entirely extinct, there is no doubt, the sensibility being supposed to be deadened by excessive alcoholism. But the heat, necessary for this combustion, is far greater than is generally supposed. It is extremely difficult to burn a dead body. That the presence of alcohol in the blood and tissues, would increase the inflammability of the dead or dying body, is possible. The commencement of the combustion, is clearly to be looked for in external, not in internal, causes. In all recorded instances, these cases have happened either in the night, or at other times when fire, candles, or matches were present, or might be supposed to be present; for frequently the evidence of this may be destroyed by the spread of the combustion itself. On the whole, it is rational to conclude, more especially as habitual drunkards are incapable of exercising care in regard to these sources of danger, that they have themselves, in a state of intoxication, set fire, in falling or otherwise, to their clothes or other combustible materials, or that they have been reached by flames otherwise occasioned by the falling of candles, or by the emission of sparks from the fire. It is significant that no case of spontaneous combustion, has ever happened in an animal.

EVOLUTION OF LIGHT.

A few examples are on record, of the evolution of *light* from certain excretions or discharges from the living human body ; but most of these instances have been observed in diseased and dying persons. The perspiration after violent exercise, in one case, and the urinary excretion in several instances, have been seen to display a decided luminosity ; in the former case, the luminous matter being even transferable to the clothing. In three instances of persons in the last stage of phthisis, a light, owing apparently to luminous breath, has been noticed playing about the features ; the surface of a cancerous ulcer is also said to have exhibited a similar appearance. In these cases, the light is supposed to proceed from the slow oxidation of phosphorus or of some phosphuretted compound, resulting from the incipient decomposition of the excretions, or from their containing some imperfectly oxidised compound of phosphorus, which had accumulated in the blood, and become eliminated in those fluids, but which would ordinarily be thrown off, in the shape of alkaline or earthy phosphates. Phosphorus dissolved in oil, injected into the veins of a dog (p. 444), produces a luminous condition of the breath ; and a luminous state of the urine has been observed in men who have taken phosphorus medicinally. It has been suggested that, as a large number of the cases of luminous breath in men, have occurred in persons addicted to excessive drinking, certain bodies, derived from the decomposition of alcohol, may impede the proper oxidation of the phosphuretted compounds, which then escape in the breath or other excretions. It is even presumed that the presence of such compounds in the blood, may impart an unusual degree of combustibility to the body. But the known compounds derivable from alcohol, even aldehyde, are not so readily oxidisable as the imperfectly oxidised compounds of phosphorus. This explanation is therefore speculative ; and the so-called cases of spontaneous combustion of the bodies of intemperate persons, as just stated, are unfounded, and capable of explanation on other and simpler grounds.

Dead animal matter is frequently *luminous* or *phosphorescent*. The surfaces of the muscles and other soft parts of bodies undergoing dissection in anatomical schools, have sometimes been seen to emit a brilliant light ; and luminous exhalations from graveyards, especially from the recently exposed soil, have not unfrequently been observed. The remains of decaying animal matter generally, may also become phosphores-

cent; but this more particularly happens in the case of marine Fishes and the marine Mollusca, Crustacea, and Cœlenterata. This is also at present attributed to a true phosphorescence, some imperfectly oxidised phosphuretted compound being supposed to be the result of an incipient stage of decomposition. It disappears on the occurrence of actual putrefaction.

The warm-blooded Vertebrata apparently possess even less power than Man, of evolving light from the living body, or authentic cases of such an event, would have been recorded. The light seen in the eyes of the cat and other creatures, in the dark, is merely a reflection from the iridescent portion of the choroid coat within the eyeball. Amongst the cold-blooded Vertebrata, the grey lizard is said to deposit eggs which are sometimes luminous; and a species of frog in Surinam, is described as emitting light, especially from the mouth. Certain cases of luminosity amongst marine Fishes, may be owing to the agitation and percussion of smaller luminous animals in the water; but a marine species of *Scopelus*, allied to the *Salmonida*, is said to emit stars of light from the body and head; it is in one of these fishes, that Leuckart has recently described scattered organs, containing lens-like bodies, which are regarded by him as eyes (vol. i. p. 604). These may be light-reflecting organs.

The most remarkable and characteristic examples of the emission of light from the living animal body, occur amongst the Non-vertebrate creatures. Some of these are met with in *air-breathing* animals. Thus amongst the *Annulosa*, two families of Coleopterous insects or beetles, viz., the *Elaterida* and *Lampyrida*, furnish us with the well-known examples of the fire-flies and glow-worms. The fire-flies proper to hot climates, give out a very brilliant light from two spots, one on each side of the thorax, and from a third on the under side of the same part; the light is present in both sexes. In the glow-worms, however, the light is softer, and though observed in the male, and, even more feebly, in the nymphal stage, in the larvæ, and in the egg, it is decidedly more striking in the female; it is also chiefly observed at particular seasons. It proceeds from the under side of the three last segments of the abdomen. Examined under high magnifying powers, the luminous patches are seen to consist of little sacs, containing a yellowish granular matter, which is the luminous substance. These sacs are closed by horny lids, having peculiar flat surfaces, suited to the diffusion of the light; the granular matter and sacs are traversed by numerous air-tubes, or tracheæ. The light is given out, even after the segments are removed from the rest of the body, and luminous streaks may be produced by rubbing the yellow matter between the fingers. There seems no doubt that the use of the luminosity, is the feeble combustion of some organic compound excreted by the animal. It is said, however, not to contain phosphorus in any appreciable quantity, and the product of its combustion carbonic acid (Matteucci). Other alleged instances of luminous winged Insects, are doubtful. Amongst the *Annulosa*, some Centipedes, and, under certain circumstances, the common earth-worm, also present examples of luminosity. Amongst the Mollusca, there are luminous *air-breathing* Gasteropods.

By far the larger number of luminous Non-vertebrate animals, is

found amongst the aquatic breathers, and exclusively, perhaps, amongst the marine species. Of the Molluscos marine animals, the Cephalopodous Octopus, the Pteropodous Cleodora, and the Lamellibranchiate Pholas, exhibit luminosity. Many Molluscoïd animals, but especially the Tunicated Salpida and Pyrosomida, are eminently distinguished for this property. Again, many minute marine Crustacea appear like little luminous specks in glasses of sea-water, especially when this is agitated; and they are even discernible in the stomachs of larger Molluscoïd animals, which feed upon them. Some of the marine Annelida are distinguished by being able to emit sudden scintillations of light along the body, which may be repeatedly excited by mechanical irritation. It has been suggested that, in these cases, the light may be excited through nervous agency, which may possibly undergo conversion into light (Carpenter). Amongst the Annuloid animals, certain Star-fishes are said to be luminous. But the Cœlenterata yield the largest number of luminous marine creatures, especially the Acalephæ and the Hydroid Polyps, such as Pennatula and others. Lastly, a minute jelly-like creature, formerly assigned to the group Acalephæ, amongst the Cœlenterata, but now classed amongst the Protozoa, by some as a Rhizopod, but by others as a peculiar and gigantic Infusorial animalcule (Huxley), the *Noctiluca miliaris*, is the most common of all light-giving creatures in the temperate oceans, and is the chief cause of the luminous nocturnal appearance in our Northern Seas. In the Tropics, the phenomenon is much more striking and brilliant, and depends upon a greater variety of animals, especially upon the Medusæ and the Hydroid Polyps.

The luminosity of these various marine animals, is said to depend upon a mucous secretion from their integument, which will even impart luminosity to water or milk, with which it is mixed. The so-called phosphorescence is always more marked in warm than in cold climates; it is increased by moderate elevation of the temperature of the water, and, most remarkably, by brisk agitation of the fluid, either because the secretion is detached from the animals, or simply owing to their excitement. The light is extinguished by extremes of either heat or cold; it disappears *in vacuo*, and is restored on renewed exposure to air; it is rendered more vivid by various stimulating substances, if moderately used, and also by electricity; but it is extinguished by the excessive employment of these, and especially by such vapours as those of ether and chloroform, which would interfere with oxygenation. Oxygen increases and maintains the phosphorescence; carbonic acid first excites, and then destroys the luminous property; sulphuretted hydrogen almost instantly arrests it. The luminosity may continue for a time after death, unless this has been produced by some specially poisonous substance. It entirely ceases as soon as putrefaction begins.

From the preceding facts, it is obvious that the luminosity of animals is owing to some living action, and not to decomposition.

Its use is by no means understood. The supposition that it serves occasionally to guide one sex to the other, affords a very partial explanation of the facts; for it does not apply to the cases of the multitudes of hermaphrodite marine luminous animals. It may conduce to their destruction, by assisting other animals in seeking them as food; or it may serve to illuminate deep waters. But this curious phenomenon affords a good example of the imperfection of our knowledge of *final causes*.

In the glow-worm, it appears not to be phosphorus, but some carbon-compound, which produces the light. Even in the case of the numerous marine luminous animals, it is not proved that the light is owing to the slow oxidation of a phosphuretted substance. This, however, seems more probable in the case of animals living in water, in which the luminous oxidation of a phosphuretted body, is more conceivable than that of a hydro-carbonaceous substance. It is possible that some, at least, of the feeble light exhibited in these phenomena, or its intensification, is due to *fluorescence* developed in a high degree; fluorescent substances certainly exist in living animals. The term phosphorescence must be regarded as descriptive and provisional only, for the light may not depend, in any case, upon the oxidation of a phosphuretted compound.

The evolution of light from these animals, as a normal phenomenon, and that from the human body, as an occasional or morbid occurrence, must be accompanied by chemical change, in which the chemical energy passes into the form of light. The photic work of the animal body, must therefore depend on the chemical energy evolved by it. But the quantity of matter subjected to change in its production, is very small.

EVOLUTION OF ELECTRICITY.

The electric currents constantly present in the living nervous and muscular tissues, and the common electric current present in the entire human body, and in the bodies of the lower animals generally, especially noticeable in the frog, have been elsewhere mentioned (vol. i. pp. 166, 281). This common current usually passes from the lower extremities to the head of an animal; but in the upper limbs of the human body, it is said to be directed from the shoulder to the fingers. Electric currents have also been detected upon different secreting surfaces and glands, and even between a secreting membrane and the veins returning from it. These phenomena cease with the life of the animal experimented upon. The direction of these currents, is shown by delicate galvanometers. Thus, currents pass from the venous blood, which is positive, to the gland or secreting surface, which is negative; no current passes between a gland and the arterial blood. Arterial blood is said to be positive, compared with venous blood (Scoutetten). Between the corresponding points of the two sides of the body, or of opposite limbs, no electric currents are ordinarily found; but they occur between non-correspondent points, and even between corresponding points, if there is a difference with respect to their nutritive activity, as when one limb is at rest, and the other in motion, or as when one limb is more or less inflamed (Matteucci, and Bois-Reymond). The electricity of the human body under ordinary circumstances, is rapidly conducted from it, and thus

an equilibrium is maintained with respect to surrounding media. But when the body is insulated, its proper electric state is speedily manifested, either when it is brought into contact with non-insulated bodies, the galvanometer intervening, or when two insulated persons are connected with the galvanometer, or touch each other. Thus examined, the electric condition of men is usually positive, that of women is said more frequently to be negative. Sanguine and irritable persons exhibit a more active electric condition, than others. It is well known that electricity is sometimes developed in the body, by friction, or by the rapid removal of stockings, especially silk ones, or other articles of dress which fit closely to the skin. This phenomenon is accompanied by slight crackling noises, and even by sparks, especially in dry weather, dry air being a better non-conductor than moist, and so preventing the escape of the electricity of the body. Remarkable and exceptional instances of the accumulation of electricity in the human body, are on record, in which, if the person were only moderately insulated sparks could readily be drawn from any part of the body.

The total quantity of electricity developed in the body, must be very large; but owing to the quantity of water in the tissues, to the high conducting power of that fluid, and to the absence of arrangements calculated to insulate the electric currents, the electricity passes as soon as it is generated, into a state of equilibrium. Moreover, this animal electricity speedily acquires a condition of equilibrium, as regards neighbouring objects and media; and it is only when the body is more or less perfectly insulated, that other than static currents can be detected in it.

Similar electric currents exist in all Warm-blooded Vertebrata, and are probably universal in the Cold-blooded Vertebrata. In the former they are remarkably strong, and the animal itself, so far as its muscular system is concerned, and probably also as regards its nervous system, peculiarly susceptible to electric influences.

It is amongst the Cold-blooded Vertebrata only, and in the lowest Class of these, viz., in Fishes, that the singular power exists, of generating and accumulating, within certain organs, a large amount of electricity which can be discharged from the body, in the form of a shock, either voluntarily or, apparently also, at the will of the animal. Electric fishes are found in almost all climates; but they belong to different genera. There are eight species known at present to possess this power. Of these, five are marine; three of these are Torpedoes, belonging to the Ray-family; they inhabit the Mediterranean and the Atlantic, and are sometimes even used as food. The fourth is the *Trichiurus*, or Sword-fish of the Indian Seas. The fifth marine species is the *Tetraodon*, found amongst the Comoro Islands. The fresh-water or river species of elect

hes are the *Silurus* or *Malapterurus*, a salmon-like fish of the Nile, Niger, and Senegal, rivers of Africa; the *Momyrus*, or Nile Pike, and, lastly, the celebrated *Gymnotus*, or Electric Eel, found only in the Amazon and other large rivers of South America.

In the *Torpedoes*, which are true flat fishes, the electric organs consist of two compressed oval masses, lying one on each side of the head, and reaching from between the gills into the body; they are supported in front and externally, by a cartilaginous border. They consist of a strong membranous investment, enclosing a soft pulpy structure, divided by septa, into hexagonal columns, which have their ends directed towards the upper and under surface of the fish. Each column is subdivided, by delicate and extremely vascular partitions, into numerous separate cells, and each cell is filled with a clear fluid, of which $\frac{1}{10}$ th part is albumen, with traces of common salt. Owing to the large proportion of water in them, the specific gravity of the electric organs, is only 1026, whilst that of the body of the fish, is 1060. These remarkable organs are supplied with very large nerves, larger than any other nerves in the body, and larger than any nerve in animals of the same size. The nerves arise from a special nervous ganglion, called the *electric lobe*, connected with the medulla oblongata, immediately behind the cerebellum; at their roots, these nerves have apparent connections with the fifth and eighth pairs; their finest branches end in close plexuses, upon the delicate partitions between the cells of the columnar portions of the electric organ. The electric organs of the *Gymnotus*, are four in number, arranged in two pairs, one larger than the other; they form one third of the entire bulk of the animal, and extend nearly its whole length. Their structure is similar to that just described in the *Torpedo*; but the prismatic columns of cells are larger, fewer in number, and of greater length, for they are placed lengthwise in the electric organ and body of the Fish. The nerves are derived, it is said, from the spinal cord only, and are upwards of 200 on each side of the body. Some of its nerves proceed from the fifth cranial nerve, but most of them, it is asserted, from the spinal cord.

In the *Silurus*, there is no such distinct electric organ; but a dense fibrous tissue, having albuminous substance contained in its interstices, surrounds the whole body, and is regarded as the homologue of the more perfect organs of the *Gymnotus* and *Torpedo*.

The power of the *Torpedo* to give shocks, is comparatively small, but they excite much pain. The shock of the *Silurus*, and of the largest *Gymnoti*, which measure twenty feet in length, is sufficient to kill small animals, and to paralyse men and horses, both as regards sensation and motion. The electric power depends upon the integrity of the nerves connected with the electric organs, as is proved by the results of partial or complete division of those nerves. Small portions of the organ, separated from the body by no other part than a nerve, still retain their electric power. Destruction of the electric lobe in the *Torpedo*, completely destroys the electric power. The discharge of electricity in the *Gymnotus*, may be caused, by touching different points on the same side of the body, or different points on opposite sides of the body; in the *Torpedo*, it is excited by touching the upper and under surface of the animal. But it is said, that when exactly corresponding points on the two

sides, or on the same surface of the body, are touched, no shock occurs and that not even a current passes through a galvanometer. Contact with one point only, induces no shock, and a *Gymnotus* instinctively endeavours to bring a second point into near relation with anything which touches it. The back of the *Torpedo*, is electrically positive; the ventral surface is negative; the strongest currents are obtained immediately over the electric organ. In the *Gymnotus*, however, the most powerful shock are obtained, by touching the two extremities of the body, which here present opposite electric states, the head being positive, and the tail negative.

The electric discharge from these Fishes, not only produces shock to the living nerves of one individual, or even of a chain of persons touching each other's hands, but it affects the galvanometer, magnetizes needles, accomplishes chemical decompositions, and even produces a spark in a properly devised circuit (Faraday). There can be no doubt, therefore, of its perfect identity with the electricity developed by physical means.

The energy of the electric discharge, depends on the size and strength of the animal. It is exhausted by too frequent use; sometimes a powerful discharge precedes death. *Torpedoes*, in which the electric nerves have been divided, appear to live longer than those the electric organs of which are subject to repeated irritation. The electric energy, like that of the vital processes generally, is greater, and less easily exhausted, in young *Torpedoes* than in older ones, and shock have been felt even from the foetal Fish, as it has been extracted from the abdomen of the parent. Just as the embryo of the Snapping Turtle has been seen to snap its jaws whilst still in the egg, so the foetal *Torpedo* has been seen to try and bring its surfaces in proper contact with foreign bodies, so as to pass the shock through them. The electric power is first excited, and then destroyed, by strychnia and morphia. A temperature of 32° suspends the power, which is again restored by immersion of the Fish in water at a temperature of from 58° to 68° ; at 86° rapid and strong discharges take place, and the *Torpedo* soon dies.

The use of this remarkable power, beyond that of serving for protection, or for obtaining food, is not evident; indeed allied Species, exposed to the same enemies, and living on the same food, flourish without such organs. Moreover, the *Gymnotus* kills many more fishes than eats, and *Torpedoes*, kept in confinement, have been found to destroy small fishes without eating them. The electric discharge has been supposed to assist indirectly in the digestive process, inasmuch as animal substances subjected to powerful electric currents, undergo ready decomposition; the intestine of the *Torpedo* is very short, but so also is the digestive canal of the allied Species. It has also been imagined that oxygen may be supplied to the gills, by decomposition of the water near them by these organs; but this is improbable. Lastly, it has been thought that they may render the Fish galvanometric, and thus enable it to recognize changes in the electric condition of the surrounding medium. The chief use, however, must surely be protective. It has been said, that certain Molluscs and Insects are able to emit feeble shocks of electricity; but this is doubtful. The Cœlenterata, as the Sea-Anemones and others, irritate and destroy their prey by stinging organs, which act suddenly, but not really electric.

The great size of the nerves distributed to the electric organs, the special distribution of the extremities of the nerves upon the membranous walls of the cells, the results of division of those nerves, and of construction of the so-called electric lobe, the excitement of the organs by irritation of the brain, and lastly, the apparent subjection of the whole apparatus to the will of the animal, show, that in some way, the electric phenomena developed in these living galvanic batteries, are largely dependent on the nervous system. According to one view, the electric force may be developed and accumulated in the electric organ, and may be merely discharged under the influence of the nerves. But it is difficult to understand, how this could happen in an organ apparently insulated, for its membranous envelope is as good a conductor as moist tissues or water. Another theory supposes, that static electric currents, similar to those which are detected in muscular tissue, but of a far more powerful kind, are constantly circulating through these organs; and that the equilibrium of such currents being disturbed by some action of the nervous system, a discharge of the electric force then takes place. In accordance with this view, the organs themselves, with their vascular cell-walls, seem constructed for a special purpose, being unlike any other known animal organ; after repeated discharges, time must be allowed for the restoration of the power of giving shocks; and lastly, the electric force is precisely proportioned to the general activity of the nutritive functions. Moreover, a difference has been observed in the character of the discharge or shock, between the Torpedo and the Gymnotus, a difference connected with peculiarities in the structure of their electric organs. The shock is more powerful in the Gymnotus, the piles of cells of the organ being extremely long; whereas in the Torpedo, the shock is less powerful, and the piles of cells are shorter. It has been supposed, by some, that the so-called nerve-force is directly converted, in these organs, into electric force; and the further inference has been drawn, that the two forces are hereby shown to be identical. The former hypothesis may be correct, but the latter opinion is not so (vol. i. p. 291). The two forces are so far related, that either most easily excites the other. The ultimate source of the electric power, is chemical action, most probably oxidation.

STATICS AND DYNAMICS OF THE HUMAN BODY.

Physiology is not sufficiently positive or perfect, as a science, to have its exact *constants*. But we may here collect certain numerical expressions, concerning the specific gravity, height, and weight of the body; the weights of its various organs; the relative quantities of its chief proximate chemical constituents; also, concerning the weight of the daily food, and its proportion to the weight of the body; its proximate consti-

tments, and the relations of these to the proximate constituents of the body ; their destination in the economy ; and the effects of deprivation of food.

Besides this, we may examine, in a general manner, the *chemical work* performed within the body ; and endeavour to estimate, numerically, its *vito-chemical* processes, and their relation, on the one hand, to the food, drink, and air, and, on the other, to the *mechanical* and *calorific* work, performed in, and by, the system. The *nutritive*, *electric*, and *nervous* work, may also be here again noticed.

STATICS OF THE HUMAN BODY

Specific Gravity of the Body.

The specific gravity of the body, depends upon that of its various tissues and organs. Essentially, all the materials of the body, with the exception of the fatty substances, are heavier than water, and the mean specific gravity of all the tissues, is higher than that of water. But the air retained in the lungs during life, even the residual and reserve air, is just sufficient to counterbalance the higher specific gravity of the body generally, and so enables it to float (vol. i. p. 227).

The specific gravities of the chief tissues are given in vol. i. p. 78 ; that of the principal organs, is mentioned in their description. The specific gravity of the entire body, with air in the lungs, is usually stated to be from 1060 to 1070. As bone is the heaviest, and fat the lightest, of the tissues, the specific gravity of the entire body, is influenced by the relative proportions of these two tissues ; hence it is greater in thin bony persons, but less than the average in children and women who are generally fatter than men, and, also, in corpulent persons of either sex. But the practical buoyancy of the body in water, is, of course, chiefly determined by the size of the chest and lungs, the freedom of the latter from congestion or deposits, and their condition of inflation. On the least inspiratory and expiratory movement, the body rises or sinks in water. Necessarily, the body is more buoyant in the sea than in fresh water. The effect of clothing, or of any kind of weight, is, of course, adverse to buoyancy.

Height of the Body.

The human body continues to grow, at least up to the age of twenty-five (Quetelet), and, as it would seem, even up to the age of thirty years (Danson). The mean height of the male in Belgium, at twenty-five years of age, is 66·1 inches, or 68 centimetres* (Quetelet). The mean height of males, at twenty-one years, in Germany, is found to be 68·1 inches, or 173 centimetres (Zeising). Measurements of 4,800 criminals, in England, give a mean height in the male, from twenty-five to thirty years, of 66·5 inches, or nearly 169 centimetres (Danson). The extreme divergence of the German measurements, must be exceptional, and due probably to too limited a number of observations. The English stature is nearer to a mean. The height of the full-grown female, at thirty years of age, is 62·2 inches, or 158 centimetres (Quetelet). The mean difference between the height of the sexes, is about 4 inches.

Weight of the Body.

The estimated average weight of the body in the male, is also rather less, according to Quetelet, than according to other observers. From thirty to forty years of age, it is 140 lbs., or 3·66 kilogrammes.† From twenty-five to thirty years of age, the mean weight of the male, according to Danson, is 143·1 lbs., or 65 kil. Vierordt adopts the result of one observation on a powerful male, aged forty-two, whose weight was about 143·5 lbs., or 65·25 kil. The weight of the female, at thirty, is 121 lbs., or 55 kil., *i.e.* about 22 lbs. less than that of the male; but the weight increases in women up to the age of fifty, when it is about 123·2 lbs., or 56 kil.

From the preceding numbers, a mean height of 5 feet 6½ inches, and a weight of 144 lbs. avoirdupois, may be assumed, for the average full-grown male. In the calculations made by English writers, on the working power of a man, 150 lbs. is, however, usually taken as his weight.

Weights of different Parts and Organs of the Body.

These are taken from Duroy and Krause, the weights given by them, having been converted into lbs. and ozs. avoirdupois :—

* A centimetre = ·3937 inch.

† A kilogramme = 2·2 lbs. avoirdupois.

	lbs.	oz.	oz.
The recent skeleton	21	8	344
Muscles and tendons	77	8	1240
Skin and subcutaneous fat	16	5	261
Brain	3	2 $\frac{1}{2}$	50·5
Spinal cord		1 $\frac{1}{4}$	1·25
Eyes		$\frac{1}{2}$	·5
Tongue and hyoid bone	3		3
Œsophagus		1 $\frac{3}{4}$	1·75
Stomach	7		7
Small intestine	1	11 $\frac{1}{2}$	27·5
Large intestine	1	1	17
Salivary glands		2 $\frac{1}{2}$	2·5
Liver	4	1 $\frac{1}{2}$	65·5
Pancreas		3	3
Spleen		8 $\frac{1}{2}$	8·5
Thyroid body and remains of thymus		$\frac{3}{4}$	·75
Blood = $\frac{1}{13}$ weight of body	11	0	176
Heart		10 $\frac{1}{4}$	10·25
Right and left kidneys		10 $\frac{1}{4}$	10·25
Larynx, trachea, and larger bronchi		2 $\frac{3}{4}$	2·75
Lungs	2	10 $\frac{1}{4}$	42·25
Unweighed parts	1	4 $\frac{1}{4}$	20·75
Total	143	8	2296

Proportions of the Proximate Constituents of the Body.

All the constituents of the body, belong to five chief categories; viz. albuminoid substances and those immediately derived from them, fats, salts, extractives, and water. The following Table shows the quantities of these substances in a body supposed to weigh 150 lbs.; and also the proportions of each in 1,000 parts (Moleschott):—

	Quantities in the body in lbs.	Proportions in 1000 parts
Albuminoid substances and their deriva- tives }	30	201
Fatty matters	4	25
Salts	14	92
Extractives	1	6
Total solids	49	324
Water	101	676
	150	1000

Daily Quantity of the Food, and its Composition.

It has been stated that a daily consumption of 2 lbs. of bread, with 12 oz. of meat, which contain 11·6 oz. of carbon, and ·7 oz. of nitrogen, will support a fully-exercised adult, (Béclard). According to another estimate, 1 lb. of meat, 1 lb. 3 oz. of bread, $3\frac{1}{2}$ oz. of fat, and about $2\frac{1}{2}$ imperial pints of water, are needed by a healthy, actively-employed man (Dalton). Vierordt's estimate, as we shall see, assigns 4 oz. of dry albuminoid matter, 3 oz. of fat, $11\frac{1}{2}$ of starchy food, and 1 oz. of salts. An ordinary English labourer is said to consume daily, a diet containing 12 oz. of carbon and 5 of nitrogen, and a dietary containing only 10·4 oz. of carbon, and ·42 of nitrogen, is stated to be insufficient to preserve his health (Ed. Smith). Cases, however, are on record, such as that of Louis Cornaro, in which a much lower diet has served to maintain life and health for very long periods. The diet of men engaged to run, walk, or row, and also that of jockeys, has occupied special attention in England; and though entirely the result of empiricism, the rules laid down, correspond generally with the suggestions of science. They usually include an excess of meat diet, a spare allowance of amylaceous and saccharine food, and a more or less strict abstinence from alcoholic beverages, tea, coffee, and tobacco. Very active exercise, sweating, sponging, early rising and retirement to rest, are also enjoined.

The daily food may be classified under four chief categories; viz. the albuminoid substances, the fatty and starchy substances, the saline or mineral substances, and the water. According to Vierordt, a healthy adult is sufficiently nourished, by consuming daily, 4·2 oz. av. of dried albuminoid substances, 3·1 of fatty matter, 11·5 of amylaceous food, and 1·1 of saline substances. Playfair has estimated that the daily diet of an active adult man is about 4·2 oz. of dry albuminoid substances, 1·8 of fats, 18·7 of starch, and 9 of mineral substances. The difference between these diets, the former preponderating in fatty matters, and the latter in starchy substances, is doubtless owing to differences of national habit. To these solid substances, viz. 19·9 oz. in the former, and 25·6 oz. in the latter diet, must be added 93 oz. of water, which, according to Vierordt, includes that taken both in the food and drink, making a total of 112·9 oz. in the first

diet, and 118·6 in the second diet. The daily amount of new material taken into the body, will, in the former case, be about $\frac{1}{20}$ th, and in the second, about $\frac{1}{15}$ th, of the total weight of the body. In the diet indicated by Vierordt, the proportion of non-nitrogenous to nitrogenous food, is as $3\frac{1}{2}$ to 1; whilst in that allowed by Playfair, it is as $4\frac{3}{4}$ to 1. But a compensation exists in the fact, that the fatty matters, in excess in the German diet, are much richer in carbon than starch; for, adopting the so-called starch equivalent for fat, which is as 2·4 to 1, and expressing the fatty matters, in both diets, as if they were starch, the disparity between them is lessened. The starch equivalent in the former diet, would then be 19, and in the latter 23, which, as compared with the amount of nitrogenous matter identical in both diets, viz. 4·2 oz., would give a ratio between the non-nitrogenous, or hydro-carbonaceous elements, and the nitrogenous, of about $4\frac{1}{2}$ to 1 in the diet of Vierordt, and of about $5\frac{1}{2}$ to 1 in that of Playfair.

The annexed Table shows these facts more clearly.

Daily food of an adult man, in ozs. avoirdupois :—

	Playfair	Vierordt	Proportions in 1000 parts (Vierordt)
Albuminoid substances . . .	4·2	4·2	37
Fatty matters	1·8	3·1	28
Salts	·9	1·1	8
Starch	18·7	11·5	103
Total solids	25·6	19·9	176
Water	90	93	824
	115·6	112·9	1000

Relations between the Constituents of the Body and those of the Daily Food.

Having determined the proportions of the different proximate constituents of the body, in 1000 parts, and the same proportions in regard to the proximate constituents of the food, and knowing that the total weight of the daily food is about $\frac{1}{20}$ th of the total weight of the body, it is easy to ascertain approximately, the ratio between the daily quantity of each of those proximate constituents of the food, and the quantity of

the same, or similar substances, present in the body. The results are shown in the annexed Table.

	In 1000 parts of the body	In 1000 parts of food	In 50 parts of food, i. e. $\frac{1}{20}$ the weight of the body	Proportion per cent. of consti- tuents of food, to similar consti- tuents in body
Albuminoids . . .	201	37	1.85	.9
Fats	25	28	1.4	5.6
Salts	92	8	.4	.4
Carbohydrates, viz., starch, sugar, ex- tractives } . . .	6	103	5.15	86
Water	676	824	41.2	6.1
Totals	1000	1000	50	

From this comparison, it appears that, in round numbers, the daily supply of albuminoid substances in the food, is rather less than 1 for every 100 parts of albuminoid materials in the body; that the supply of fat, is $5\frac{1}{2}$ parts for every 100 in the body; that salts, less than $\frac{1}{2}$ a part; and of water, 6 parts only for every 100. On the other hand, the proportion of the carbohydrates in the food, as compared with the small quantity of substances of similar composition in the body, is as much as 86 per cent. This obviously suggests that the amyloid and saccharine substances are not largely employed for conversion into tissue, but have some other function in the economy, one of which, there is reason to believe, is to supply fuel for the purposes of generating chemical force, to be transformed into animal motion and heat. These, indeed, are the so-called calorific substances, *heat-givers*, or *respiratory* food, as distinguished from the albuminoid substances, *plastic* food, or *flesh-formers*. From the small percentage of these latter bodies, daily supplied to the system, it is evident that not more than $\frac{1}{100}$ th part of such substances in the body, can, on an average, be replaced by nutritive metamorphoses in one day. Hence, we arrive at the conclusion, that 100 days, at least, are necessary, supposing waste and supply to be equal, for the complete transformation of all the albuminoid, and their derived constituents, in the living body. But the actual rate of metamorphosis is so different in the several albuminoid tissues, as *e.g.* in muscular, as compared with tendinous, tissues, and moreover, so inconstant, that no safe

conclusions can be arrived at upon such general data. The fatty matters of the body, are possibly changed in much less time.

It is difficult to estimate the ordinary daily waste of the human body. It has been shown, however, that the daily quantity of food, necessary to maintain an animal at its normal weight, is more than twice the weight of the daily loss which it undergoes, when deprived of all food. When the weight of the food, is only equal to the loss during temporary starvation, the animal continues to lose weight, and the egesta given off by the alimentary canal, the kidneys, the skin, and the lungs, weigh more than the quantity of food taken. This has been attributed to the requirements of the processes of digestion, which demand the formation of copious secretions containing much solid matter; but as most of them are reabsorbed, it is more probably to be explained by the fact that, in a starving animal, the waste is reduced to a minimum, and that the effect of insufficient food, is to excite the system to an unaccustomed activity, and to loss by metamorphosis. Nevertheless, during health, with sufficient food, and in a sufficiently long period, there must be an actual balance between the loss and the supply.

Destination of the Food in the Living Economy.

This subject includes two points of investigation—viz. the *intermediate*, and the *ultimate*, *chemical changes* or *metamorphoses* of the different proximate constituents of the food. The latter point may be first examined.

In order to arrive at the *ultimate* destination of the proximate constituents of the food, after these have compensated for the waste of tissue, or have been consumed in furnishing force for imparting motion and heat, it is necessary to determine the intrinsic composition of those constituents, and that of the various excreted matters. The chemical constitution of the *ingesta* which pass into the body, must be compared with that of the *egesta* which pass from it—two terms of an equation, which, if our means of experiment, and our knowledge were exact, should be shown precisely to correspond. This comparison has been attempted by Vierordt, as shown in the following Tables, in which the quantities, given by him in grammes, have been reduced to ozs. avoirdupois:—

A. Ingesta during 24 hours, in ozs.

Food, drink, and air	Quantities consumed	H ₂ O of starch, and water	C	H	N	O	Salts
Albumen	4.23		2.29	.28	.66	1	
Fat	3.17		2.47	.36		.34	
Salts	1.13						1.13
Starch	11.63	6.46	5.17				
Water	93	93					
Oxygen of air }	26.24					26.24	
Totals	139.4	99.46	9.93	.64	.66	27.58	1.13

B. Egesta during 24 hours, in ozs.

Excretions	Quantities excreted	Water	C	H	N	O	Salts
Breath; Carbonic acid and Water . . .	43.4	11.66	8.79		?	22.95	
Perspiration; do. do.	23.62	23.3	.09			.23	
Urine { Urea							
Water	62.31	59.98	{ .24	{ .07	.56	.41	.92
Extractives			{ .1	{ .03			
Solid excreta . . .	6.07	4.52	.71	.1	.1	.43	.21
Water formed in the system . . .	} 4.			.44		{ .27	
						{ 3.29	
Totals	139.4	99.46	9.93	.64	.66	27.58	1.13

In Table A, the quantities of the various constituents of the daily food, solid and fluid, are the same as those quoted in 535. The daily amount of oxygen introduced into the system, calculated from the quantity known to be given off, in that period, as carbonic acid from the lungs and skin. The quantities of hydrogen and oxygen which exist in the carbohydrates, the proportions to form water, are set down as water.

In Table B, the ultimate destination of all the chemical elements of the constituents of the food, is traced. The totals under each head in the two Tables, correspond, the decimals having been, in some cases, slightly altered in the reduction

of grammes into ounces. The upper row of the figures which refer to the urine, represents the elements of the urea; the lower row, those of the non-nitrogenous urinary constituents. Above two thirds of the hydrogen of the food, are converted in the body, into water, partly by uniting with oxygen already in the food, but chiefly by combination with oxygen from the air. The remainder of the oxygen, unites with carbon, to form the carbonic acid of the pulmonary and cutaneous exhalations. Of the entire excreta, 32 per cent. pass off by the breath, 17 by the skin, 46.5 by the kidneys, and 4.5 by the alimentary canal. The ultimate products of the chemical metamorphoses of the food within the living body, are regarded essentially as *urea*, *carbonic acid*, *salts*, and *water*. The small residue consists chiefly of nitrogenous and other matters in the faeces and of epithelial, and epidermoid, losses.

The *intermediate* stages of metamorphosis, which occur as the food is assimilated into blood, or solid tissue, and the further exceedingly complex, and only imperfectly known, change which these undergo, have been followed, more or less completely, in describing the composition and use of the different kinds of food (p. 2-7), the modes of their assimilation (p. 174), the office of the several constituents of the blood (p. 287), and the sources of the biliary and urinary pulmonary excretion (pp. 354, 377). A summary or general view of these metamorphoses, may now be given.

Water appears to undergo no decomposition into oxygen and hydrogen; rather it is increased by additional water set free, or actually produced, by the union of oxygen and hydrogen, in the body itself. It is probably concerned in processes of hydration and dehydration, thus effecting changes in the more complex elements of the body.

The *saline* substances of the food, pass, for the most part, unchanged through the body, and reappear again in the excretions, especially in the urine; but the chlorides must undergo temporary decomposition for the formation of the hydrochloric acid of the gastric juice, the chlorine, however, again meeting with appropriate bases. Additional saline matters appear in the excreta, besides those in the food, chiefly alkaline sulphates, formed by the oxidation of the sulphur in the albuminoid compounds of the body, and magnesian phosphates, resulting from the oxidation of the phosphuretted fats of the blood corpuscles and the brain. The ammonia in the breath, in the perspiration, and in the urine, and also the urea, ur.

acid, and hippuric acid, are saline substances, the products of decomposition of one or more nitrogenous matters in the body.

The carbohydrates, starch, and sugar, are changed, the first into sugar, and both, probably after transitional mutations, into lactic, oxalic, or other acids. Their elements are ultimately traceable, the carbon, in the carbonic acid of the breath and perspiration, and the hydrogen and oxygen, in water. Sometimes starch or sugar may give rise, apparently by an upward metamorphosis, to biliary or other fatty acids, and thus to fat, which may then be deposited in the tissues as fat, or they may protect and thus spare the fat already in the body. Sugar and starch given with meat or albuminoid food, produce obesity; they are even more fattening than fat itself, as they are more easily oxidised, and act more effectually as protectors to the other constituents of the body. Ultimately, their elements are, in any case, subjected to the same oxidising processes, yielding *carbonic acid and water*. Their upward transformation is probably exceptional, because they are more easily oxidisable than fat.

The *fatty* matters, or hydro-carbons, are usually decomposed into their fatty acids and glycerin, before they enter the chyle, and are probably recomposed there, or in the blood; possibly, also, they are again decomposed, under the influence of the alkaline constituents of the blood, on the eve of being oxidised. This oxidation may be direct or immediate, into carbonic acid and water; but the fat may be first employed, perhaps in the formation of the choleic acid of the bile, or of the volatile fatty acids of the milk, butyric, capric, and caproic; or it may be still further resolved into propionic, formic, or acetic acids, and so pass to the ultimate condition of *carbonic acid and water*. The hydrogen of fat, being in excess of its oxygen, and not in the proportions to form water, as in the carbohydrates, this element and the carbon, which also exists in excess, demand, for their reduction, a much larger relative supply of oxygen from the air. Hence, in regard to vito-chemical calculations, the fat may be represented by a *starch equivalent*, 1 part of fat being equal to 2·4 parts of starch. A minute portion of fat may remain almost unoxidised, in the form of cholesterin. Fat, like the carbohydrates, also saves the metamorphosis of the albuminoid tissues and food; for if an animal be fed on insufficient animal diet, to which some fat is added, there is less waste, and a smaller consumption, of nitrogenous matter than if it be fed on a scanty meat diet without fat. A normal pro-

portion of fat in the food, also saves the consumption of meat; for the weight of an animal is then maintained with one third or one fourth less meat, than when it is fed on meat alone. An excess of fat in the diet, however, has, as its chief result, an increase of weight, by accumulation of adipose tissue. The most successful plan of fattening animals, is not to withdraw the albuminoid foods, but to allow these to remain the same in quantity, and to increase the hydrocarbons and carbohydrates. The researches of Lawes and Gilbert, show that in the fattening of animals, much more fat is produced than there is fat in the food, only $\frac{1}{9}$ th, or $\frac{1}{3}$ rd being contained in the food, and therefore, from $\frac{2}{3}$ rds to $\frac{8}{9}$ ths being produced from other sources, largely from the carbohydrates, but also from any excess of nitrogenous food, after the albuminoid tissues are supplied. This is especially the case, if the non-nitrogenous food be defective, or if an animal be fed on flesh only (Voit.)

Alcohol, which may be considered as one type of hydrocarbonaceous food, has been said, by some, to escape wholly unchanged, by the breath and the excretions; but it is generally believed to be, at least, partly oxidised, either with or without previous conversion into aldehyde, acetic acid, or some other intermediate substance or substances. It is not supposed to contribute directly to the formation of tissue, not even of fat. It is not essential as an article of diet; it may even be detrimental, by its chemical action on albuminoid substances, hardening and precipitating them, or by its physiological action, stimulating or even poisoning the nervous system, or producing slow and insidious changes in the blood, the tissues, and the secreting and excreting organs, which render the system unable to resist injury or disease; it may even lay the foundation for irremediable organic changes in the brain, heart, bloodvessels, liver, and kidneys. In smaller and more moderate quantities alcohol, however, is probably oxidised in the blood, and so serves for the development of motion and heat. It restores a feeble pulse, quickens the vascular action, and so raises, for a time, the vital activity of all the functions, vegetative as well as animal. Much difference of opinion exists as to the claim of alcohol to be regarded as an aliment, of course of the non-nitrogenous class. Alcohol certainly enters the circulation but its effect on the blood is not understood, though it has been supposed to render that fluid thicker, and the blood plasma less fit for penetrating the tissues. Persons have been known to live long periods on alcoholic beverages, but not on pur-

alcohol, unless this was accompanied by small quantities of bread or other food. So also persons who drink much beer become fat, but spirit drinkers do not. It has been supposed to be possibly nutrient to the nervous system, but this is not established, and its plastic properties may be doubted. Whether it may act by saving tissue, through its own oxidation, or whether it may serve as respiratory or calorific food, depends on its ability to undergo oxidation in the system. According to Lallemand, Perrin, and Duroy, it leaves the body entirely, and unchanged; this view is also, in some measure, supported by Dr. E. Smith. By these authors, alcohol has been found *unchanged* in the blood, in the various organs, specially in the liver and the cerebro-spinal nervous centres, and also in the breath, the perspiration, and the urine; moreover, they have not found aldehyde, nor acetic or oxalic acids, into which alcohol has been said to be changed in the body. It has also been shown that aldehyde, if administered, is itself unstable in the system, and appears as acetic acid. But the quantities of alcohol found in the excretions, do not appear to have been accurately compared, by those observers, with the quantity actually taken into the stomach. Baudot and Thudicum have shown that when this is done, the quantities eliminated are proportionally small. Even in the results obtained by Lallemand, Perrin, and Duroy, only $\frac{1}{4}$ th of the alcohol taken, is thus accounted for (Gingeot). In these cases, and also in those in which enormous quantities have been given in disease, more or less alcohol must therefore be appropriated, or assimilated, by the tissues, be retained in them, or be oxidised. The administration of alcohol does not increase, but diminishes, the temperature (Perrin, Dumeril, Demarquay, Ringer, and Rickards), and also the quantity of carbonic acid gas evolved (Lehmann, Vierordt, Hammond, Böcker, Lallemand, and Dr. E. Smith). The quantity of urea excreted, is likewise diminished. Duchek and Mialhe supposed, that this was owing to the formation of aldehyde, or some other compound not so perfectly oxidised as carbonic acid; but this is hypothetical. The effect seems rather to be due to its lowering, in some manner, all those organic processes, which lead to the formation of carbonic acid by the disintegration of blood and tissue (Moleschott, Carpenter); in this way, alcohol may retard waste, and conserve power. It may also favour the formation of new tissue, and save the combustion of fatty matter (Hammond).

Albuminoid bodies, the most complex substances in the animal

economy, undergo, as might be supposed, the most complicated intermediate changes, before they are ultimately resolved into their simplest excretory products. Albumen itself, constituting the pabulum of the tissues, does not undergo any upward chemical metamorphosis; all its changes are necessarily retrograde. Slight modifications, perhaps of hydration, convert it into albuminose, pepsin, salivin, and pancreatin. Equally slight oxygenation probably changes it into globulin, fibrin, syntonin and casein; this, together with a loss or total deprivation, of sulphur, is concerned in the production from it of keratin, chondrin, and gelatin; the disappearance of the sulphur, must be an essential step in the nutrition of the gelatin-yielding tissues. The substitution of iron, perhaps, for hydrogen or carbon, with a loss of oxygen, is possibly the mode of derivation of the cruorin, or blood pigment, from albuminoid matter; whilst the other pigments, pulmonary, cutaneous, biliary, and urinary, especially abound in carbon, and may be formed by processes of dehydration. The nitrogenous acid of the nervous substance, cerebrie acid, is probably derived directly or indirectly, from some breaking up of albumen, but this peculiar acid, which contains phosphorus, exists in Indian corn and other food; the glycocoll and taurin of the glycocholic and tauro-cholic acids of the bile, also, perhaps, proceed from the dissolution of albuminoid substances; and it is more than probable that glycogen, or animal starch, and taurin, are formed in the liver, likewise, by the splitting up of albumen.

In this case, the glycogen contains the carbon, with hydrogen and oxygen in the proportions of water, whilst the choleic acid, with the glycocoll and taurin, contain, besides those elements, the nitrogen and sulphur. The formation of gelatinoid substances from albumen, which must happen in nutrition, liberates sulphur, which may either be oxidated, or find its escape in the taurin of the bile. Albumen may even be a source of common fat; for the biliary acids might easily give rise to oleic and other fatty acids. During the changes due to the development of the eggs of the limnæus or water snail, the percentage of albumen in the ova, after drying, is said to be diminished from 95·2 to 91·8, whilst that of the fatty matter is increased from ·6 to 2·2; the percentage of salts is increased from 4 to 6 (Burdach.) It is further alleged that albumen is resolvable into glycogen and urea, a change which is supposed to be the origin of the sugar formed in the system in diabetes at least when no starch or sugar is taken in the food (Haugh-

on). In this case, the albuminoid matter is supposed only to have been assimilated into the blood, not to have entered into the formation of tissue.

If albumen be broken up in the liver, then its non-nitrogenous products are resolved into *carbonic acid* and *water*; the sulphur appears in the alkaline sulphates, except when it passes off as dyslysin in the solid excreta, whilst the nitrogenous bodies ultimately reach the chemical condition of *urea*. But the more obvious metamorphosis of the albuminoid bodies, that which consists of a series of retrograde chemical changes to more oxidised nitrogenous bodies, such as creatin, creatinin, leucin, tyrosin, inosinic acid, sarcin, xanthin, hippuric acid, and uric acid, by which path they ultimately reach the condition of *urea*, a substance identical with cyanate of ammonia, and which has also been regarded as a carbamide or a carbide of amidogen, which contains carbon, hydrogen, nitrogen and oxygen. The ammonia found amongst the saline constituents, is probably always derived from a further breaking up of urea.

Albumen may be artificially decomposed, by acids or alkalies, or by spontaneous changes, into leucin, tyrosin, and glycoll, all which nitrogenous compounds are found in the body, especially in venous blood, and in the liver and spleen; whilst creatin, creatinin, and inosinic acid, are found in actively exercised muscles, and in the blood. Creatinin is, of all these substances, the nearest to urea, and is readily converted into it by assumption of the elements of water. Urea itself has been found in the muscles of certain fishes. *Gelatin* and the gelatinoid substances, behave in their downward metamorphoses like the albuminoid bodies, yielding especially urea, but no sulphur compounds. It is doubtful whether they ever undergo an upward metamorphosis into albumen; but they may spare the waste of this, and may save, and even nourish, the gelatin-yielding tissues. Large quantities alone are useful for this purpose; when much gelatin is taken in the food, the urea is increased in the urine, the specific gravity of which has been known to rise to 1034.

One important inference from our present knowledge concerning the chemistry of the food in the body, is this: that all food may be either oxidised after being merely absorbed, or assimilated into the blood, as well as after its constituents have been converted into tissue. This is sufficiently obvious as regards carbonaceous and hydrogenous food, or the respiratory

food; but it is equally true of the plastic albuminoid and gelatinoid substances. The excretion of urea is not so much increased by muscular exertion, as was once supposed, but is largely augmented by an excess of nitrogen in the food. Smith, Voit, Lehmann, Fick and Wiscilenus, and others. The excess of any substance in the food, beyond that which is necessary for the tissues and for respiration, is known as *luxus consumption*, or *diet of luxury*; it reappears in an increased excretion of urea, carbonic acid, and water.

Interesting deductions may be drawn, from comparing the destination of the food in the Herbivorous and Carnivorous animals. In the Herbivora, a very large proportion of the carbon, hydrogen, and nitrogen, of the food, passes off undigested from the alimentary canal; whilst in the Carnivora, nearly all the food constituents are absorbed into the chyle or blood. Of the carbon which thus enters the blood, the ratio of that given off by the lungs and skin, to that excreted by the kidneys, in the Herbivora, about as 30 to 1, whilst in the Carnivora, the proportion is only as 10 to 1. Of the hydrogen absorbed a greater relative proportion is also found in the cutaneous and pulmonary excretions, in the Herbivora, viz. 25 to 1, as compared with the urine; but in the Carnivora, the proportion in the urine, as compared with the breath, are reversed, being as 3.25 to 1. The nitrogen, in the Carnivora, passes almost exclusively into the urine, the proportion to that in the skin and lungs, being as 99 to 1; in the Herbivora, the ratio is only as 1.5 to 1. The excreta in a Carnivorous animal, represent so the excreta of an animal fed on a pure flesh diet; but those of an Herbivorous animal, exhibit the results of an excess in the proportion of the carbohydrates, viz. an increased activity of the pulmonary and cutaneous exhalations.

It must further be observed that the quantities of the albuminoid substances, or their derivatives, removed in a solid form from the body, in the mucus and unused secretion of the digestive canal, in the epithelium from other mucous membranes, and with the epidermis, nails, and hair, are very small, and escape all active metamorphosis.

Finally, the sum of all the chemical changes in the body, is *oxidation*. The carbon of all the carbohydrates and hydrocarbons, appears as *carbonic acid*, and their hydrogen and oxygen, as *water*. A portion of the carbon, hydrogen and oxygen, of the decomposed albuminoid bodies, also appear in the excreta, as *carbonic acid* and *water*; but a considerable

portion of these elements, with the nitrogen, is discharged in the form of *urea*. The sulphur and phosphorus produce their respective oxygen acids. For these changes, a larger amount of oxygen, beyond that contained in the body, is needed; and this is supplied by the atmosphere in respiration. It has been computed, that 100 parts of dried meat require 167 parts, by weight, of oxygen, for their disintegration in the body. The results appear as 182 parts of carbonic acid, 52 of water, and 31 of urinary products; whilst only 2 parts escape unchanged from the alimentary canal. No pure carbon, hydrogen, or nitrogen, is evolved from the body, but only chemical combinations of these elements, with oxygen, or with each other. Ammonia is one of these. The minute quantities of carburetted and sulphuretted hydrogen, sometimes disengaged, are probably direct products of the decomposition of the food, and not the results of vito-chemical processes. Of the carbon, 8·8 oz. are evolved as carbonic acid from the lungs, nearly 0·1 oz. from the skin; 0·34 oz. escape by the urine, and 0·71 oz. by the solid excreta. All the nitrogen appears in the two latter excretions, 0·56 oz. in the former, and 0·1 oz. in the latter.

The so-called respiratory, calorific, or heat-giving, elements of the food, chiefly enter the blood, and there undergo oxidation; whilst the plastic, histo-genetic, or tissue-forming elements, unless taken in excess, first build up the blood corpuscles and the solid tissues, and then undergo oxidation; but these latter in reality contain fat and often sugar, which may be immediately oxidised in the blood; and so even an albuminoid diet, may in that case, act as respiratory food. This must be the case in starving men and animals, in animals fed on a pure flesh diet freed from fat, and, to a certain extent, in all carnivora. On the other hand, the carbohydrates are probable sources of fat; and fatty matter is essential to plastic or histo-genetic processes. The distinction of the two classes of food is therefore, as previously stated, inexact; even the respiratory food is more or less assimilated, as it enters the chyle and the blood, and both the blood and the chyle are fluid parts of a tissue. Hence even respiratory food is plastic, as regards these fluids.

Effects of Deprivation of Food.

When an animal is entirely deprived of food, or when the quantity supplied is insufficient to compensate for the waste of

the tissues, the weight of its body gradually diminishes, and it ultimately dies of *inanition* or *starvation*.

The phenomena attending this condition, have been best studied by Chossat.

The surface of the animal's body, looks paler and withered, and the skin seems wrinkled, owing to the disappearance of adipose tissue. The secretions become more scanty and concentrated, hence the mouth is parched, and the digestive fluids wanting; but the gall-bladder becomes distended with thick tenacious bile. From the first, the urine is scanty and strongly acid. The feces are much reduced in quantity, are composed almost entirely of greenish biliary matter, and, shortly before death, contain an excess both of water and salts.

Nutrition is interrupted or arrested. A warm-blooded animal becomes after a time, restless and excited, and continues so till the last day of life; a sudden fall in its temperature then occurs, and it passes into a state of almost complete insensibility. Birds, in this condition, no longer attempt to fly; they sometimes gaze at surrounding objects, sometimes seem to be asleep. The pulse and the respiration become gradually slower, and the limbs cold. The general debility increases, until at length, being unable to stand, the animal falls over on one side, and does not again move. Diarrhœa always comes on during the last twenty-four or forty-eight hours of life, and is attended with a peculiar fetid odour of the body, a sign that decomposition is commencing. The condition of stupor gradually becomes more profound, dilatation of the pupil ensues, and the animal dies, death being sometimes ushered in by violent contractions of the muscles of the back, so that the body is drawn backwards, a condition known as *opisthotonos*.

All the organs of the body suffer loss both in volume and weight, though in very different degrees. Death usually occurs when the animal has lost about $\frac{4}{10}$ of its weight. In many cases, however, the loss of weight is equal to more than $\frac{1}{2}$, and in others to only $\frac{1}{5}$ of the weight of the body. This appears to be almost entirely dependent on the quantity of fatty tissue contained in the body, before food is withheld, the loss of weight being greater, the larger the amount of fat previously in the system.

In animals which had lost $\frac{4}{10}$ of their weight, it was found that of the fat had disappeared, $\frac{7}{10}$ of the spleen, $\frac{5}{10}$ of the liver and pancreas, $\frac{4}{10}$ of the heart, muscles, and alimentary canal—the latter at the same time having undergone considerable shortening— $\frac{3}{10}$ of the kidneys, $\frac{1}{10}$ of the respiratory organs, $\frac{1}{6}$ of the bones, $\frac{1}{10}$ of the eyes, and only $\frac{1}{50}$ of the nervous substance. Of the adipose tissue, the fat cells remain, the contents alone being re-absorbed. The diminution in the quantity of the blood, is very great, about $\frac{3}{4}$ of it disappearing. Young and thin animals suffer much less loss of weight, but they die sooner.

The duration of life appears to be but little affected, whether the animal be allowed to drink, or whether it be totally deprived of water. It has, however, been shown that, if a dog be kept without water, its tissues and organs lose weight, almost in the same proportion as if it had been deprived of solid food, with one exception, for there is little diminution in the adipose tissue. Every tissue becomes drier; but the

andular organs and the brain do not suffer so much as the other parts. There can be no doubt that the drinking of water in starvation, prolongs animal life. The smaller Mammalia, and Birds, if they are at the same time deprived of drink, usually die in nine days. Cold-blooded animals are a long time without food; frogs have been known to survive nine months.

As shown by experiments on Birds, the effect of starvation, is to diminish the average temperature for the first few days slightly, but as death approaches, very rapidly, the fall being, in the last twenty-four hours, about 25° . The greatest waste of tissue occurs in the fat, whilst the nervous system scarcely experiences any loss; so that the lowering of the temperature, and the fatal result, seem to be due to the loss of oxidisable material, and not to a destructive waste of the nervous energy. The fatty nervous substance may support itself at the expense of the adipose tissue; and this may, in part, account for the great waste of the latter. The effects of exhaustion in long continued fevers, may be similarly explained. The use of fat, as a restorative in the case of starving animals, seems to be, that it interposes an easily oxidisable substance, and so diverts the process of oxidation from the albuminoid tissues; and, in ordinary cases, it preserves the fat already stored up in the body.

In the human subject, *death from starvation* is, though rarely, not too frequently observed. At first, there is acute violent pain over the region of the stomach, which is relieved by pressure. In the course of twenty-four or forty-eight hours, this passes off, and is followed by a sensation of weakness and sinking, which is principally felt over the same part. The mouth becomes dry and parched, the breath is hot, the eyes are wild, burning, and glistening, and there is sometimes a distressing feeling of cold over the whole body. One of the most characteristic symptoms of starvation, is the intense *thirst*, which now supervenes. The entire body becomes reduced to a skeleton, the prominences of the bones are visible; the face is pale and corpse-like; there is sinking of the eyes and cheeks. A state of extreme debility ensues, so that the individual, in attempting to walk, totters like a drunken man. He is unable to make any effort, and sometimes has been observed to whine and burst into tears. The voice gradually becomes feebler. The weakness increases in intensity, and delirium supervenes. A peculiar fœtid odour emanates from the body, the surface of which becomes covered with a brownish offensive excretion. Occasionally, the mucous membranes of the different openings of the body, become red and inflamed. The psychical functions are variously affected; sometimes imbecility, at others idiocy, is induced. During the famine in Ireland in 1847, mania, which, according to Rostan, forms a prominent symptom in

starvation, was never observed (Donovan). A fit of maniacal delirium, or an attack of violent convulsions, frequently, and, indeed, commonly, precedes death.

The bodies of persons who have died from starvation, present signs of great emaciation, with dryness of the skin, all the fat of the adipose tissue, and so much fluid, having been absorbed. The stomach and intestines are empty, and, like the other large viscera, contracted and reduced in size; their mucous membrane is occasionally found ulcerated. The coats of the small intestine, become very thin and almost transparent, a condition considered, by some, as quite characteristic of death from starvation. All the organs, except the brain, are almost destitute of blood. The large vessels connected with the heart and lungs, are collapsed and empty. The gall-bladder is distended with bile, and the neighbouring parts are much coloured with this fluid, from post-mortem transudation. In some cases, the eyes are open, and exhibit an intense red colour, as if they had been highly inflamed, resembling what is sometimes seen in persons who have died from exposure to cold. Decomposition of the whole body, quickly takes place.

The time that a Man can live without food, has been variously estimated. It is generally supposed that a healthy person, deprived of both solid and liquid food, would die in from seven to ten days. Cases, however, are on record of men who have lived more than three weeks, without touching solid food.

DYNAMICS OF THE HUMAN BODY.

The chemical processes continually occurring in the nutrition and waste of the living animal body, throw light upon many other phenomena which take place in it. Besides these vito-chemical processes, it exhibits various *dynamic* acts, viz. *purely dynamic*, as in the performance of certain internal and external mechanical work, by nervo-muscular action; *thermic*, as in the evolution of animal heat; *electric*, as exemplified in the currents of electricity which constantly play through all living nervous and muscular substance, and in the more powerful discharges of the electric fishes; and lastly, *photic*, illustrated by the evolution of light in the lower animals. The living animal body is, according to this view, a machine, in, and by, which certain *physical work* is performed.

In the *Inorganic* world, chemical, dynamic, thermic, electric and photic phenomena, are also continually occurring. They

are always manifested in connection with certain changes in the condition of a material substratum, or *matter*, and modern physicists have arrived at the conclusion, that, however different these phenomena may be from each other in their outward manifestation, they may be referred, not to a different force in each case, but to correlated forces, or to *one force*, or *energy*, capable of acting in many convertible modes. Each mode of manifestation of force, has been experimentally shown to be capable of giving rise to the others, or rather of changing into them; for it disappears in so doing, and *equivalent quantities* of those other modes of action, are then called into play. Thus, for example, arrested mechanical motion, or friction, produces a proportionate quantity of heat; whilst heat, in the expansion of water into steam, gives rise to motion. Chemical action, in the explosion of gunpowder, produces motion, heat, and light, and doubtless also electrical phenomena, whilst the movingannon-ball develops heat as it strikes the target. Electricity also will give rise to chemical action, motion, heat, and light, and so on. Heat and all these other actions, are modes of motion, either of the masses or of the molecules of matter. In the various conversions of one into the other, there is neither loss nor production, but merely a transmutation of force.

In the *Organic* world, similar manifestations of force occur: chemical, dynamic, thermic, electric, and photic. The *material substratum* concerned, consists of carbon, hydrogen, nitrogen, sulphur, phosphorus, oxygen, and so forth, all being elements which exist in the inorganic world. The phenomena are invariably produced, only in connection with certain changes in the condition of these elements and their compounds. Hence, it seems probable, first, that these organic manifestations of force, are likewise correlated within themselves; and, further, that they are also correlated with the corresponding manifestations of force displayed in the inorganic world; that they are the same both in degree and kind; and that they are both derived from a common cosmical energy, the organic modes being, for a time, operative in a special sphere of action, but returnable again to the inorganic store.

By including, in one view, the Vegetable and Animal Kingdoms of the Organic world, the conversion of inorganic materials into organised matter, and its restoration back to the inorganic world, may be readily traced. The carbonic acid, the ammonia represented in the urea, and the water, which, with certain salts, are the ultimate products of the vitæ-chemical

processes of animal life, are the very substances needed for the nutrition of plants. They are themselves actually unorganised, or inorganic; they are assimilated and *deoxidised* by growing plants, under the influence of solar light and the formative agencies of the vegetable cells, and, besides building up those cells, they are combined into all the higher chemical products necessary for the food of animals, whether amyloid, oleoid, or albuminoid. The Herbivorous animals, supported by these products, transfer them to the Omnivorous and Carnivorous animals, including Man himself. By animals, as we have seen, these various products, *oxidised* by the air, once more revert to the same simple chemical compounds destitute of organisation. Now, the elementary substances, which enter into the ascending or *progressive* metamorphoses in plants, pass out, after their *retrogressive* metamorphoses in animals, with all their properties and qualities unchanged. Engaged in the organic vortex, vegetable and animal, they still retain their nature. However frequently subjected to this temporary diversion from the inorganic state, they are unchanged. It is difficult to suppose that in their condition as parts of organised bodies, vegetable or animal, they manifest mere *similitudes* of their inorganic forces, which they afterwards lay aside; but it is easy to comprehend, that they may carry with them, into their new position, *all* their properties and energies, and exercise them in the manifestation of those phenomena, which are identical in both Departments of Nature.

The methods and reasoning employed in physical research, in the examination of the various external natural phenomena, may be applied to the study of the corresponding phenomena in physiological science. As physico-chemical action, in the inorganic world, is correlated with mechanical work, heat, electricity, and light, so, in the organic world, vito-chemical changes may equally be associated with nervo-muscular or dynamic, thermic, electric, and photic phenomena, and even with the actions usually referred to the so-called nervous force. Thus, a chemical change of blood or tissue, or of both, is essential to muscular and nervous action, to the development of animal heat, to the electrical phenomena of living bodies, and to the evolution of light in animals. So, too, certain mechanical work, performed exclusively within the animal body, must, when completed, pass into heat, as the result of arrest, concussion, or friction. Heat, again, is necessary for the solvent processes accompanying the digestion and absorption of the food; and

it exercises a well-known influence upon, and often determines, the quantity of the chemical change and dynamic work performed in the body.

In the Inorganic world considered exclusively, gravitation and solar heat are the chief modes in which force is manifested. The evaporation of water from the surface of the earth, its conversion into clouds, its descent in the form of fogs, rain, snow, or hail, the formation of glaciers, mountain-streams, and rivers; and the production of ascending, descending, and horizontal currents in the atmosphere, are the evidences of these forms of energy. Oxidation and other chemical changes, though not absent, are comparatively inactive in the present condition of the inorganic world.

In the Organic world, however, in plants and animals, chemical change constitutes the most essential modes or forms of force, and the source of the other forms of force manifested by them. Under the influence of certain of the solar rays, differing from the simply heating rays, viz. the luminous and the actinic rays, the deoxidation and fixation of certain elements, take place in plants; and in these elements so fixed and combined, a force, derived from the solar rays, is then stored up. In animals, again, oxidation is the essential phenomenon, an opposite chemical change occurs, the force stored up in the animal blood or tissues, which is but a transfer of that of the vegetable constituents of the food, is, together with the force proper to the oxygen of the air, then liberated, and, by the special organic apparatus of the animal body, is changed, as required, into other modes of action, muscular, nervous, thermic, digestive, or excretory, necessary for the maintenance of animal existence. In supplementing the mechanical forces of nature dependent on gravitation or solar heat, such as wind- and water-power, Man has had recourse to chemical change, as a source for the production of heat and mechanical force. The carbon and hydrogen of coal are made to unite with oxygen; from this combination, heat is evolved; by this, water is converted into steam; and, by the expansive force of the latter, the requisite motion is obtained. An obvious comparison is here suggested between a machine and the body, between the force obtained by the combustion of dead matter and the oxidation of the living tissues; and, lastly, between the working of a steam engine and the muscular movements.

In general physics, results, to be of scientific value, must be expressed numerically. The quantity of fuel and oxygen

undergoing change in combustion, is accurately determined by weight or volume; the relative amount of heat evolved, is ascertained and recorded; and if the heat be applied, as by expansion for mechanical purposes, the value of the work it performs is exactly measured. By such means, the amount of each kind of force manifested, is expressed in numbers, so that their mutual equivalents, when they are transformed one into the other, can be determined. The introduction of this method into the domain of physiology, necessitates the determination of the quantity of matter undergoing change by oxidation, and of the work performed by it, in the living body. The results, however incomplete, are full of interest and promise.

In comparing the animal body with a machine having its source of power in combustion or chemical changes, it is usual to make this distinction: in the latter, the force is entirely derived from the combustion of substances introduced into the machine, and acts upon parts of the machine, themselves passive in the work; whereas in the former, the parts of the machine not only perform the work, but, to a certain extent, their very matter undergoes the changes by which the force is produced. In the steam engine, the heat and the mechanical work are produced by the direct transformation of fuel distinct from the machine itself; in the animal frame, the warmth and motor force are evolved from the direct transformation of the fluids and solids of the living apparatus. As will be hereafter seen, the quantity of work accomplished, in proportion to the amount of chemical change which takes place, is far greater in the animal body than in the most economical steam engine.

But, although the solids or fluids of the animal machine undergo chemical metamorphoses, as the indispensable condition of its action, the waste occasioned by those changes, is, necessarily, ultimately supplied from the food. If food be taken in excess, as in the *luxus* consumption, it undergoes oxidation in the blood, without passing into tissue; if the quantity be normal, it enters both the blood and the tissues, and then becomes oxidised; lastly, if food be withheld, the blood and the tissues undergo oxidation, they having been themselves derived from previously assimilated food. The *food* is, in the last resort, the source and measure of the *power* engendered, as a consequence of oxidation in the body. Accordingly, exact numerical estimates of the work accomplished in the human body, must refer both to the amount of combustible or oxidisable material in the *food*, and to that of the products of its oxidation found in the *excretions*.

The two most obvious forms of work performed in the living human body, are the *proper dynamic* or *mechanical* work, and the *calorific* work. Besides these, however, there are the *nutritive* work, and the *mental* work. The *mechanical* work is *nervomuscular*, and is associated with *electric* work. Some of it is *internal*, such as that of the respiratory muscular apparatus, especially of the diaphragm and intercostal muscles, of the organs of circulation, the heart and arteries, and that of the pharynx, œsophagus, stomach, intestines, and other internal muscular organs. Other internal mechanical work is that performed by the muscles which maintain the position of the body, by the muscles of mastication, and by those of the organs of speech and sense, and also the tonic contraction of the whole muscular system. A very large part of the mechanical work is, however, ordinarily *external*, such as is manifested in the movements of *locomotion* and *labour*. The proportion of the internal to the external work, in a labouring man, is as 2 to 1. The *calorific* work relates to the formation of heat; this is generated, as we shall see, either, in part, directly through the oxidation of respiratory food, and, in part, indirectly from the ultimate transformation of the mechanical work of the body into heat; or, according to some, it is entirely derived from the latter source. The *nutritive* work is the digestive, absorptive, assimilative, and secretive work, liquefacient or solidificient, often dialytic, attractive, or repellent. The *mental* work is that which is involved in the operations of the brain, acting as the bodily organ of sensation, emotion, and thought. The volitional work of the brain, and the non-volitional work of the spinal cord and ganglia, in controlling the voluntary and involuntary muscles, cannot be separated from the external and internal mechanical work performed by those muscles. Besides the *electric* work in Man and in animals generally, special electric work is performed by many animals, and *photic* phenomena are manifested by a few.

In considering the relations between these forms of work in the human body, and the source of the power in the oxidation of the food, the following data, belonging to physical science, are usually employed, the calculations being expressed in the French metrical system, which so readily adapts itself to such uses.

Measure of Heat, or Heat-Unit.

The thermometer merely shows the *relative* temperature of solid, fluid, or gaseous substances. The *actual quantities* of heat, necessary to pro-

duce changes of temperature, are determined by the apparatus known as a *calorimeter*; and the quantity needed to impart, to a definite portion of water, a definite warmth, is taken as a quantitative standard. Thus, quantity of heat which will raise the temperature of 1 gramme (1 cubic centimetre, or 15·543235 grains) of water, 1° centigrade (1·8° Fahrenheit), is named a *heat-unit*, or *calorie*. Ten such heat-units will raise the temperature of 10 grammes of water also by 1° C.; but, acting on smaller quantities of water, they will raise their temperatures proportionally, as, for example, 5 grammes by 2° C., and 10 grammes by 1° C., and so on, of 100's or 1,000's of heat-units.

Mechanical Coefficient, and Mechanical Equivalent of Heat.

Heat may produce work which is internal and direct, as in the liquefaction of solids, e.g. in the melting of metals, and the turning of ice into water, or in the conversion of fluids into vapour, as of water into steam, or in the mere expansion of fluids or gases, as of mercury or air; but heat may, also, act externally and indirectly, as occurs in the employment of the expansive force of steam in machines or engines of various kinds. The quantity of work performable by heat, is very remarkable. Thus, starting from the heat-unit previously determined, it has been shown by Mayer, Joule, Clausius, and others, that such a heat-unit, viz. the quantity of heat which will raise the temperature of 1 gramme of water by 1° centigrade if utilised by being converted into mechanical work, is equal to the lifting of the same weight of water, viz. 1 gramme, to a height variously estimated at, from 421 to 433 metres, 424 metres being the number usually adopted. Conversely, the same force will lift 424 grammes, 1 metre high; or twice that number, viz. 848 grammes, half a metre; or half that number of grammes, viz. 212, to a height of 2 metres, or 10 grammes, 4 metres, and so on for other quantities, larger or smaller. The mechanical *coefficient* of heat, is therefore 424, and the mechanical *equivalent* of 1 heat-unit, is expressed as 424 *metre-grammes*. For large weights, *metre-kilogrammes* are used; and it is here that the decimal notation of the metrical system, is so useful. Thus 1 kilogramme of water (1,000 grammes) requires 1,000 heat-units, to raise its temperature 1° centigrade; and these 1,000 heat-units will lift the same weight of water, viz. 1 kilogramme, 424 metres high; or, conversely, 424 kilogrammes, 1 metre high; 212 kilogrammes, 2 metres; or 106 kilogrammes, 4 metres high, and so on. The mechanical equivalent of 1,000 heat units is expressed, therefore, as 424 *metre-kilogrammes* (met. kils.).

In English works, the scale of temperature employed is that of Fahrenheit, of which 1·8° are equal to 1° cent.; the weight is the lb. avoirdupois, of which 2·2 are equal to 1 kilogramme, and the measure of height is the foot, of which 3·28 are equal to 1 metre. The mechanical equivalent of a given quantity of heat, is expressed in *foot-pounds*. Thus the heat which will raise the temperature of 1 lb. of water, 1° Fahr., will lift the weight, viz. 1 lb., to a height of 772 feet, or 772 lbs. to a height of 1 foot, and so on; hence the mechanical coefficient of heat, in this system, is 772, and its mechanical equivalent is expressed as 772 *foot-pounds* (ft. lbs.). To reduce the English ft. lbs. into the French met. kils., divide the former by 7·216, which is the number obtained by multiplying the

number of pounds in a kilogramme, by the number of feet in a metre, viz. 2.2×3.28 . On the other hand, met. kils. multiplied by 7.216, are changed into ft. lbs.

Not only is heat convertible into mechanical work, but mechanical work may be reconverted into heat, and the same equivalents, as before, express the ratio between them. Thus a mechanical force equal to lifting 1 kilogramme of water 424 metres high, will, when employed in friction, blows, or otherwise, develop a temperature equal to 1,000 heat-units, or will raise the temperature of 1,000 grammes, i.e. of 1 kilogramme of water, 1° cent. In friction, for example, according to the physical theory, so ably expounded by Tyndall, that heat is a vibratory motion amongst the molecules of matter, the resistance arrests, to a certain degree, the motion of *masses* of matter rubbed against each other; but the visible motion so disappearing, is transferred to the *molecules*, and so causes the invisible motion known to us as heat. The frequency of these vibrations, increases in proportion to the sensible heat produced.

Quantities of Heat developed by the Chemical Process of Combustion.

In order to be able to determine the relation between chemical force and mechanical work, it remains to be ascertained, what is the amount of heat evolved by the combination of proportional quantities, or atomic weights, of two or more elementary substances. The heat evolved in the combustion of charcoal with oxygen, is thus measured, the heat itself being supposed to be the result of an almost infinitely rapid motion of the combining molecules, through almost infinitely minute distances. Experiments made on the amount of heat imparted to water in a calorimeter, have established the fact, that very different amounts of heat are given off by burning equal weights of different combustible bodies. The mode of estimating these varying quantities, is, by measuring the heating effects produced by the combustion in oxygen, of 1 gramme weight of each substance, upon the standard gramme of water employed in the calculation of the heat-units (Favre and Silbermann). In this way, 1 gramme of carbon, in combining with oxygen in the act of perfect combustion, to form carbonic acid, evolves as much heat as will raise the temperature of 8,080 grammes of water, 1° cent.; in other words, evolves 8,080 heat-units. Again, 1 gramme of hydrogen, in uniting with oxygen to form water, evolves 34,462 heat-units. Now, carbon and hydrogen are the two chief combustible or oxidisable elements of the food, the blood, and the solid tissues; the nitrogen passes out of the body unoxidised, but combined in the urea. Most of the carbon and hydrogen escape from the system, completely oxidised, as carbonic acid and water; but some of each of those elements, especially of the carbon, appear combined with a little oxygen, and also with the nitrogen in the urea. Moreover, the quantity of heat given out by combustible bodies, appears to be the same, whether they are oxidised slowly or rapidly. The physical data just explained, may therefore be applied to the quantitative examination of the relations between the chemical changes occurring in the human body, and the amount of mechanical and calorific work performed in it.

Calorific Work of the Body.

The number of heat-units given off by a dog in 24 hours, having been ascertained to be 393,000, the number evolved in the same time, by a Man weighing seven times as much as the dog, would be 2,751,000 heat-units (Despretz). From calculations of the number of heat-units given off by the body in various ways—by radiation, by evaporation of water, and by the warming of the respired air and excreta—it has also been estimated that the daily loss, and therefore the daily production of heat by it, amounts to 2,700,000 heat-units (Helmholz).

Comparison of the Daily Amount of the Animal Heat, with the Quantity of Carbon and Hydrogen oxidised in 24 Hours.

Now, the quantity of carbon in the daily food, according to Table A at p. 539, is 9.93 oz. or 281.2 grammes; the quantity of hydrogen, not already combined with its due proportion of oxygen in the carbohydrates is 0.64 oz. or 18.86 grammes. Deducting from these, the quantities of those elements contained in the urine and solid excreta, Table B viz. 1.05 oz. or 29.8 grammes of carbon, and 0.2 oz. or 6.3 grammes of hydrogen, there remains a residue of 251.4 grammes of carbon, and of 12.56 grammes of hydrogen, free for conversion into carbonic acid and water. The 251.4 grammes of carbon, multiplied by its heat coefficient 8,080, produce 2,031,312 heat-units; whilst 12.56 grammes of hydrogen multiplied by its heat coefficient 34,462, give 432,842 heat-units, the total being 2,464,154 heat-units (Vierordt). This calculation shows a deficit in the heat, derivable from the combustion of the daily food, as compared with that given off daily by the body, of about 286,800 heat-units, or about $\frac{1}{10}$ only of the total estimated quantity of heat given off in the day. It has been supposed that the heat evolved by the sulphur and phosphorus oxidised in the body, would go far to meet this deficit. But in 120 grammes of albumen, the supposed daily supply there are only 1.4 grammes of sulphur; and, as the heat coefficient of this element, is 2,307, the heat from that source, provided all the sulphur were oxidised, which is not the case, would only amount to about 32,300 heat-units; the phosphorus would yield a somewhat smaller number. Moreover, there are considerations which would appear to make the deficit still worse. Thus, although the hydrogen of the starchy food, is excluded by Vierordt, because, being present with oxygen in the proportions to form water, it is probably already so combined, and therefore unable to evolve any further heat of combustion, yet no deduction is made for such hydrogen as may be balanced by the oxygen in the fatty and albuminous food. In this fat and albumen, besides the oxygen which passes out with the urea and the solid excreta, sufficient exists to unite with, and so neutralise about, 2 grammes of hydrogen; and if it be so combined, a loss of heat power must be admitted, of about 68,900 heat-units. A small quantity of the carbon and hydrogen of the food, also disappears unoxidised as carburetted hydrogen. It is, further-

more, usually maintained, that a certain quantity of chemical action is transformed into external mechanical work, without being converted into heat in the body; and this quantity has been estimated as high as 235,000 heat-units. From these circumstances, the total deficit in the heat-units of the food, as compared with those supposed to be given off from the body, would be 500,000, i.e. between $\frac{1}{2}$ and $\frac{1}{6}$ of the daily heat.

This discrepancy may, however, be fully explained, by possible errors in the larger data. Thus, the estimated weight of the human body, and therefore the number of heat-units producible by it, in proportion to the particular dog experimented upon by Despretz, may be too large; or the daily supply of carbon and hydrogen in the food, may be underrated for a man of the estimated weight. Vierordt himself elsewhere assumes only 2,500,000 heat-units as the average daily quantity evolved by an adult; and the same number has been accepted by Carpenter as the probable number for a man weighing 180 lbs., i.e. much above the average standard. The adoption of this number, would reduce the deficit to 300,000 heat-units, which would be provided for, by a daily addition of 37 grammes of carbon in the food, a quantity which would be contained in 3 oz. of starch, or $1\frac{1}{2}$ oz. of fat. According to Playfair's Tables (p. 563), such an additional quantity is actually consumed. The results of improved methods of research and calculation, therefore, quite support Lavoisier's chemical theory of animal heat.

Mechanical Work of the Body.

The daily working power of a Man, and the actual mechanical work done, according to his individual strength, must vary greatly according to the exercise or labour he undergoes. It is said that a Man can raise 600 lbs., 1 foot in a second, for 8 or 10 hours in the day; that, on level ground, he can draw 640 lbs. weight; that he can lift 286 lbs. with both hands, and support on his shoulders, 330 lbs. The daily work of a Man, is said to be between $\frac{1}{7}$ and $\frac{1}{8}$ of that of a horse. More exact computations show, that with severe labour, the daily work of a Man is equal to 207,871 met. kils. or 1,500,000 ft. lbs. (Ranken); with moderate labour, it is not more than 66,518 met. kils. or 480,000 ft. lbs. (Ranken). The work performed by pedestrians, has been estimated at 109,570 met. kils. or 790,720 ft. lbs. (Haughton). In marching, a soldier exercises a tractive force equal to $\frac{1}{20}$ of the weight of his body, arms, and accoutrements. The coefficient of traction, is therefore expressed as being $\frac{1}{20}$ of the weight to be moved; hence a soldier weighing 150 lbs. with 60 lbs. of weight to carry, and marching 14 miles per day, performs work equal to 107,560 met. kils. or 776,160 ft. lbs. (Playfair).

Thus, $150 + 60 \div 20 \text{ lbs.} \times 14 \times 5,280 \text{ feet} = 776,160 \text{ ft. lbs.}$

The mean of 9 estimates of laborious work, according to various authorities, is 105,605 met. kils. or 762,048 ft. lbs. This represents the daily *external* mechanical work of the body. Of the *internal* mechanical work, a large portion, which is usually referred to the external work, is that which poises the body and supports it. Next to this, is the true internal work, of which the most is performed by the heart, which has been estimated by one authority at 37,871 met. kils. or 273,280 ft. lbs.

(Haughton); and by another at 70,000 met. kils. or 492,520 ft. lbs. in 24 hours; the daily work of the left ventricle alone, is estimated at 46,000 metre-kilogrammes (Vierordt). Another estimate gives 43,000 met. kils. for the left ventricle, and 21,000, for the right ventricle, making a total of 64,000 (Donders). According to the lowest estimate, the work of the heart, which is always beating, is equal to more than $\frac{1}{3}$, and, according to the highest, to nearly $\frac{2}{3}$, of the total daily external work. Taking the highest estimate of the heart's work, and adding it to the mean labour-work of Man, as above estimated, we arrive at the sum of about 175,600 met. kils. To this must also be conjoined, the work of respiration, i.e. of the diaphragm and the intercostal muscles, 63,000 met. kils. (Donders), the work of the digestive organs, and other internal mechanical work, which will probably raise the total daily mechanical work, external and internal, performed by a man engaged in active employment, to the sum of 250,000 met. kils. From other calculations, Vierordt adopts 200,000 met. kils. but exclusive, as it would seem, of the internal work. Again, the actual mechanical effort or work accomplished by a muscle, is equal to the product of the weight lifted, multiplied by the height to which it is lifted. Thus, with a frog's muscle, Weber found that 5 grammes were lifted 27.6 millimetres 15 grammes 25.1 mm., 25 grammes 11.45 mm., and 35 grammes 6.4 mm. The products of these numbers, showing the work accomplished in each case, are respectively 138, 376, 286, and 220 *gramme-millimetres*. Hence, although the work effected, at first increases with the load, it soon reaches a maximum, and then diminishes. Since every muscle becomes exhausted by work, and requires intervals of rest for reparation it is necessary, in order to determine the actual mechanical work accomplished by a Man or animal, to take into account the element of *time*. In this way, it has been estimated that the mechanical work of a Man, is represented by 7 met. kils. per second, and that of a horse, by from 6 to 70 met. kils. Allowing 8 hours work out of the 24, the daily work of a Man would be 201,600 met. kils. (Redtenbacher). The average work per second, throughout the day, would be 2.3 met. kils.

In the steam engine, the amount of heat evolved by the fuel consumed, is sometimes 30 times, and, in the most economical engines, 2 times, greater than the quantity converted into useful mechanical work. Theoretically, the utmost available mechanical power is only $\frac{1}{10}$ part of that producible by the heat of the coal consumed. But in the human body, the economy of combustible material is much greater. The total amount of heat given off from the body, in 24 hours, has been shown to be from 2,500,000 to 2,750,000 heat-units. The former or smaller quantity would lift a corresponding number of grammes, or 2,500 kilogrammes, to a height of 424 metres; and would therefore yield a mechanical equivalent of about 1,060,000 met. kils. or about 5 times as much as that which is requisite for the total daily work, viz. 250,000 met. kils. Whilst, therefore, in an engine, $\frac{1}{20}$ part only of the fuel consumed is utilised as mechanical power, $\frac{1}{5}$ of the food absorbed by Man is so appropriated. This latter proportion agrees with Helmholtz calculations.

Relations of the Kinds of Food, to the Modes of Work.

The calorific and mechanical work of the body, being thus understood to have their immediate source in the power stored up in the food and in the oxygen of the air, and which is set free on the occurrence of chemical combination between them, after such food is assimilated into blood or tissue,—it may be admitted that, allowing for certain errors of calculation and deficiencies of knowledge, the numerical or quantitative method shows that sufficient matter is oxidised in the body, to account for *both* those modes of work. It must, however, next be enquired, what are the relations of the *different kinds of food* to these *two different modes* of work.

It has long been observed, that the carbon in the carbohydrates and hydrocarbons, or amyloids and oleoids of the starchy food, greatly exceeds that contained in the nitrogenous or albuminoid food. In Table A, p. 539, the ratio is shown to be 7·64 to 2·29, or rather more than 3 to 1; the number of heat-units developed by the former, would of course be proportionally large. If to this carbon, be added the hydrogen united with oxygen, this portion of the food seems to be the obvious source of *calorific* power in the body. Vierordt remarks, indeed, that, if from the carbon and hydrogen of the nitrogenous food, enough of those elements be deducted to form the urea excreted by the kidneys, a quantity remains, totally insufficient to develop the heat-units necessary for the calorific work; for then only 57·3 grammes of carbon and 6·3 grammes of hydrogen, will be left, which, multiplied by their heat coefficients 8,080 and 34,460, yield a total number of 680,082 heat-units, which is only about $\frac{1}{4}$ of the required daily amount, viz. 2,500,000. The non-nitrogenous food, in accordance with the general opinion, is, therefore, regarded as the essential source of the *animal heat*. Indeed, 22 oz. of starch alone, not an unusual quantity in certain daily dietaries, Table, p. 663, would yield 2,187,000 heat-units.

As regards the *mechanical work*, it is well-known that this, whether internal or external, involuntary or voluntary, is performed through nervo-muscular action; that this implies fatigue and waste of the muscular and nervous substance; that so long as muscular contractility lasts, so long do oxidation changes go on in a muscle (G. Liebig); that a due supply of oxygenated blood is necessary for the continuance of this con-

tractility; and that the quantity of carbonic acid contained in the venous blood returning from muscles, is in direct proportion to their activity. It is further certain that the muscular and nervous tissues must be largely supplied by the nitrogenous or albuminoid portion of the food. From these facts, it might well be inferred, that the mechanical or nervo-muscular work of the body, has its immediate source in the transformation and oxidation of the muscle itself, and, therefore, in the so-called histogenetic, plastic, or flesh-forming nitrogenous food. The opinions and practice of agriculturists, railway contractors, and trainers of men destined for athletic sports, further indicate, that a proportional increase in the quantity of flesh-forming food, is believed to be necessary for animals or men engaged in severe or protracted labour.

The teaching of Liebig, on these points, is indeed very precise and decided. According to him, the hydrocarbons and carbohydrates are the exclusive heat-formers; whilst the sole source of mechanical power, the oxidation of the nitrogenous substance of the muscles and nerves built up again by the albuminoid or plastic constituents of the food. These views have been very generally accepted, and have been especially supported, amongst others, by Ranke, Draper, Playfair, and Odli. Draper says of muscular contraction, that it may be supposed to be due to the disintegration of the sarcous particles, and that the transformation of muscle by oxidation, may be the condition of muscular action. Odli regards the combustion of the carbon and hydrogen of fat, as liberating a force exhibited solely in the form of heat; whilst the combustion of an equal quantity of the carbon and hydrogen of voluntary muscle is expressed chiefly in the form of *motion*.

Playfair has endeavoured to show, on numerical grounds, that although the chemical combination of the carbon and hydrogen of the albuminoid food, with oxygen, is insufficient to account for the calorific work, yet it is adequate to produce the mechanical work of the body. Hence he concludes that it is the ultimate magazine of force, for the production of dynamical operations. The following are the principal facts and arguments to which he directs attention.

From numerous English and foreign sources, he has collected a series of dietaries actually in use, under various conditions of rest or work, of which the annexed Table A, gives only the mean results. The *starch equivalent* includes the actual starch of the food, together with the carbon and hydrogen of the fat, expressed as starchy matter, 1 part of fat being considered equal to 2·4 parts of starch. The *subsistence diet*, is that which is considered necessary to support life in a condition of rest, or a diet necessary for the vital mechanical work of the body; it is illustrated by the convalescent diet of hospitals, and by the low diets of ill persons. The diet needful for active employment in health, is represented by the diet of soldiers during peace. An improved diet necessary for more arduous work, is that given to soldiers during war. The diet of active labourers, is exemplified in that of the corps of Royal Engineers.

engaged in civil employment. Lastly, a still fuller diet, is that of labourers and others employed in yet more continuous and heavy work.

A. Mean results of Dietaries in oz. avoirdupois.

	Flesh-formers	Fat	Starchy substances	Starch equivalent	Salts	Carbon and flesh-formers	Carbon and heat-givers	Total Carbon
Subsistence diet	2.33	.84	11.69	13.68	—	—	—	7.469
Soldiers' diet } during peace }	4.215	1.847	18.69	22.059	.714	2.267	9.72	11.987
Do. during war	5.41	2.41	17.92	23.48	.68	2.9	9.81	12.71
Do. in civil } work }	5.08	2.91	22.22	29.38	.93	2.73	12.113	14.844
Diets of la- } bourers }	5.64	2.34	20.41	25.97	—	—	—	13.89

B. Average Quantities in oz. of different Food Constituents, consumed under different conditions of rest and work (Playfair).

Food Constituents	Subsistence diet	Diet in quietude	Diet of healthy adult	Diet of active labourers	Diet of hard-worked labourers	Addition required for active labourer
Flesh-formers	2.0	2.5	4.2	5.5	6.5	3.5
Fat	0.5	1.0	1.8	2.5	2.5	2.
Starch	12.0	12.0	18.7	20.0	20.0	8.
Starch equivalent	13.2	14.4	22.0	26.0	26.0	12.8
Carbon	6.7	7.4	11.9	13.7	14.3	7.

The *subsistence* diet in Table B, is supposed to show, amongst other acts, the quantity of albuminoid food consumed in the performance of the absolutely *essential internal* mechanical work of the body, when at complete rest. Taking this as a *datum* quantity, the additional amounts consumed in quietude, in full health, in active labour, and in hard labour, are .5, 2.2, 3.5, and 4.5 oz. In extreme labour, the quantity of flesh-formers, is, therefore, more than trebled, as compared with the subsistence diet. The starch equivalent is also increased, being, however, only doubled. This increase, Playfair considers as coincident with the additional animal heat given off in increased exertion, during which all the functions, digestive, assimilative, circulatory, and respiratory, are much excited. An increased consumption of non-nitrogenous food, is not only demanded by an increased waste of the nitrogenous tissues, but it may even cause the latter, by exciting the animal functions. As, for an active labourer, 3.5 oz. seems to be the additional amount of albuminoid food needed beyond the subsistence diet, so a horse, when at work,

is said, by Playfair, to consume 27 oz. more nitrogenous food than when at rest. The proportion between these superadded quantities, in the Man and the horse, is about 1 to $7\frac{1}{2}$, and, as already mentioned, the horse's daily work is estimated as being equal to that of 7 or 8 men. It is further stated, that the work of a horse, is to the work of an ox, as 1.43 to 1; whilst the total albuminoid food consumed by those two animals, when engaged in labour, is as 1.46 to 1. In animals fed exclusively upon a flesh-diet, allowance being made, when necessary, for the fat contained in it, Bischoff, Pettenkofer, and Voit, found that the carbon excreted in the urea, is about $\frac{1}{4}$ th of the quantity given off in the form of carbonic acid; hence Playfair supposes that 1 part of albumen, if oxidised by 100 parts of oxygen, may be transformed into 3.1, or about 3 parts, of urea, which would contain 3 of carbon, into 21 parts of carbonic acid, which would contain 21 of carbon, and into 13 parts of water. The carbon in the urea and carbonic acid, is, here also, as 1 to 7. Urea itself is regarded as a compound of carbonic oxide and ammonia, and its carbon, as being only partially oxidised. Of the hydrogen, three-fourths are deducted, as being either already combined with oxygen, or as belonging to the ammonia. The heat-units are accordingly calculated for so much carbonic acid, carbonic oxide, and water, and also for sulphuric acid formed by the sulphur of the albumen. One ounce of albumen, 437.5 grains, or 28.35 grammes, if thus decomposed, would yield 126,500 heat-units, the mechanical equivalent of which, is 53,762 met. kils. Hence the 2 oz. of flesh-formers in the subsistence diet, would afford 107,524 met. kils. of work, which exceeds the essential vital work performed in the body in the condition of convalescence, the work of the heart representing the largest item of the internal mechanical or vital work, being taken at 37,781 met. kils., which, however, is too small an estimate. Again, the $3\frac{1}{2}$ oz. of additional albuminoid food consumed by the active labourer, are mechanically equivalent to 188,167 met. kils.; whilst the mean amount of laborious work, is only equal to 105,605 met. kils. Lastly, the $5\frac{1}{2}$ oz. of albuminoid food consumed by the active labourer, yield 295,691 met. kils.; whereas his total mechanical work, external and internal, is, as we have seen, only 250,000 met. kils. Even if each of the above-mentioned mechanical equivalents of the albuminoid food, be reduced by one-twelfth, for that which passes off in the solid excreta without undergoing combustive change, still, in each case, enough power remains, derived from the oxidation of the albuminoid food, to execute the mechanical work, whether internal or external, performed by the body.

It is maintained by Playfair, that the blood cannot be the source of the motor power, but this opinion is open to question. The quantity of fat in muscular tissue, only 2 per cent., is too small to accomplish it. The fat in the heart, could only yield 10,157 met. kils., whilst the work of the heart is estimated as equal, at least, to 37,780 met. kils. In 4 oz. of dried flesh, there would be 150 grains of fat, which would yield 36,888 met. kils., whilst that amount of muscular substance itself, would yield 214,544 met. kils. The fat of muscle being therefore wholly inadequate to produce the mechanical work, it is presumed, by Playfair, that the larger quantity yielded by the muscle itself, must be regarded as its source. Moreover, the fatty substances, as we know, are wanted for heat-giving purposes. They are required, we may add, to supply the

waste of the nervous substance in muscular action; and the fat in the muscles, may protect them from oxidation, when no movement is taking place; but fat alone cannot act vicariously as a substitute for albuminoid food. In starving animals, the fat wastes gradually day by day, undergoing oxidation at an equal daily rate, whilst the muscle wastes irregularly, at first slowly, then more uniformly, but, at the approach of death, very slowly indeed, the mechanical work, external and internal, being reduced to a minimum.

The amount of albumen allowed in the dietary of Vierordt (p. 539), after deducting the urea, and $\frac{1}{12}$ th for loss by the solid excreta, would yield 680,000 heat-units, or a mechanical equivalent of 264,152 met. kils., a quantity closely corresponding with the amount obtained by Playfair's calculations, and likewise exceeding the estimated total daily mechanical work of 250,000 met. kils.

The small balance of unemployed force, is regarded by Playfair as proving the extreme economy of the operations of the living body. If, indeed, the mechanical work derived from the chemical energy developed in the oxidation of $3\frac{1}{2}$ oz. of excess of albuminoid food, viz. 188,167 met. kils., be compared with the external mechanical work of an actively employed labourer, 105,605 met. kils., the proportion of actual work to the total producible energy is about as 1 to $1\frac{4}{5}$. In comparing the total work performed, 250,000 met. kils., with the total heat produced from all the food, 295,691 met. kils., more than $\frac{5}{6}$ th of the chemical energy developed is utilised, instead of $\frac{1}{5}$ th, as estimated by Hehmholz, and others, and instead of $\frac{1}{20}$ th, as is the case in the best steam-engines. Every particle of energy developed in the body, is probably, in some way, usefully employed.

The researches of the Rev. Dr. Haughton on excreted products, taken as the measure of work, bear on this question of the source of motor power in the body. By determining the quantities of urea excreted by the kidneys, under different circumstances of rest and labour, he endeavours to ascertain the potential energy represented by the urea, considered as a product of the decomposition of the albuminoid tissues. The work of the body, is classified, by him, into vital, mental, and mechanical. These he supposes to be represented respectively, by the daily excretion of 297, 217, and 136.5 grains, making a total of 650.5 grains of urea; the total daily amount excreted by a person engaged in very active bodily and mental work, is, therefore, 650.5 grains. In routine labour, he infers that 400 grains of urea are sufficient to represent the vital and mechanical work; but, in higher work, he allows 533 grains of urea; and regards 575 grains, as the average for a healthy actively engaged adult. As 1 part of urea represents 3.1 parts of dried albumen, this daily average quantity of urea, viz. 575 grains, represents 3.9 oz. of dry albuminoid food; 400 grains, 3 oz.; and 650 grains, 4.3 oz. This quantity is thus ap-

portioned by Haughton; for the vital work, 297 grains, representing 2 oz. of albumen; for the mental work, 217 grains, representing 1·4 oz.; and for the mechanical work, 136·5 grains, representing ·9 oz. To raise these quantities into the actual quantities of albuminoid food consumed, $\frac{1}{12}$ th more must be added, in each case, for the albumen eliminated, unchanged, in the solid excreta. Then it will be seen that the quantity of urea taken to represent the vital work, is more than equal to the flesh-formers in the subsistence diet of Playfair. But the quantity said to correspond with the external mechanical work, is insufficient, representing, even with an addition of $\frac{1}{12}$ th, less than 1 oz. of albuminoid food; whilst the mechanical work of an active healthy adult, demands, according to Playfair, an extra quantity of 2·2 oz. of flesh-formers, beyond the subsistence diet. The large quantity allotted to mental work, is perhaps excessive, and may supply the deficiency; for the quantity of albumen corresponding with the total amount of urea, is 4·4 oz.; this, with its superadded $\frac{1}{12}$ th, would more than equal the full diet of Playfair, though it would not approach the 5·5 oz. diet of the active, much less the 6·5 oz. of the hardworked, labourer.

But the estimates of Haughton, as to the quantity of urea excreted daily under conditions of labour, are less than the quantities which have been observed by others. The quantity in convalescence, and in cases of starvation or hunger-cure ranges from 263 to 300 grains; the average quantity in health appears to vary from 560 to 580 grains; and the quantity excreted daily, by hard-worked labourers, has been found to differ, according to their work and *food*, from 600 to 700 or 800 grains. In Hammond's experiments on himself, whilst without exercise, the quantity of urea excreted daily, was 487 grains, and of uric acid 24·9 grains,—the quantities of those two substances excreted in moderate exercise, were 682·1 grains and 13·7 grains; and, in hard exercise, as much as 865 grains and 8·2 grains. The quantity of urea which corresponds with 5·5 oz. of albuminoid food, the active labourer's diet, is 733 grains. The estimates of Haughton are evidently low; if augmented, in accordance with the observations of others, as to the increase in the urea excreted during full exercise, and *with a full diet*, they might, at first, appear to harmonise with the view, that the chemical energy developed by the oxidation of the albuminoid food, is the source of all the mechanical work performed in the body. The production of the urea, i

not supposed, by itself, to develop the energy required; but this substance is an index to the quantity of albuminoid substance oxidated, in the body, into urea, carbonic acid, water, and sulphuric acid. This urea can be easily separated and weighed; but the carbonic acid and water, derived from the partial oxidation of the albuminoid food, mixing with the much larger quantities derived from the carbohydrates and hydrocarbons, completely escape measurement.

But the theory of Liebig (1842-51), as to the special source of the motor power of the system, thus illustrated by arguments and calculations, derived from an advanced state of knowledge concerning the relations between chemical action, heat, and motion, is opposed by many authorities, especially by Mayer, Traube, Donders, Heidenhain, more recently by Fick and Wislicenus, and, in England, by Lawes and Gilbert, and by Frankland. The experiments of Lehmann, Ed. Smith, Voit, Bischoff, Speck, and Dr. Parkes, have assisted much to elucidate this subject.

It was long ago maintained by Mayow, of Bath (1681), that, for the occurrence of muscular action, combustible material, fat, must be conveyed by the blood to the muscles, together with some principle derived from the air in respiration. According to Mayer, of Bonn (1845), an early observer in the field of quantitative research as regards heat and its relations to other forms of force, a muscle is not the material by the chemical change of which, mechanical work is produced; but an apparatus by means of which, the transformation of force is accomplished. If the former were true, he argues that the heart would be completely oxidised, in doing its own work, in 8 days. He believes the capillaries of the muscle, to be the seat of the actual changes, and the blood to be the fuel consumed. Traube also has distinctly taught, that the substances, by the burning of which, force is generated in the muscles, are not the albuminoid constituents of those tissues, but non-nitrogenous substances, either fats or carbohydrates. Donders and Heidenhain coincide in these views.

It has, moreover, been found that the amount of urea excreted, is regulated, not so much by the exercise taken, as by the quantity of albuminoid food which is consumed. Hence much of this substance must be formed independently of the metamorphosis of muscle; and therefore Haughton's estimates of it, as a measure of work, become seriously invalidated. Lastly, much uncertainty prevails, as to the accuracy of the data employed for the calculations of the heat given off in the oxidation of albuminoid food, and, therefore, as to the correctness of the deductions from them, made by Vierordt, Playfair, and others. Thus, Lawes and Gilbert (1852) observed, that of two pigs fed, one on lentils, which contain 4 per cent. of nitrogen, and the other on barley, which contains only 2 per cent., the excreta of the former yielded twice as much nitrogen as those of the latter; from which they infer that the quantity of urea excreted, *i.e.* of albuminoid substance decomposed, is no index to the amount of work done, the exercise taken having been the same in each case, but that it depends on the quantity of nitrogenous

food consumed. They, moreover, conclude that some of the muscular power depends on the oxidation of non-nitrogenous substances. Again the researches of Edw. Smith, Voit, Lehmann, Bischoff, and Parkes indicate that the urea excreted, bears no definite relation to the labour performed; and that in prolonged exercise, the increase of urea is very small. The effects of treadwheel labour, serve only to increase the quantity of urea, by 19 grains in 24 hours, as compared with that eliminated in easy labour (Smith). In fasting animals, the effects of increased exertion are also very slight as regards the urea, and seem to be regulated by the periods of ingestion of water, and by the increased respiration and circulation, rather than by the direct waste of the voluntary muscles (Voit, Bischoff).

Lastly, the experiments of Dr. Edw. Smith prove, on the other hand, that the production of carbonic acid does increase, strictly in accordance with the exercise taken. During sleep, the quantity exhaled in an hour was, in his own case, 19 grammes; whilst lying down before sleep, 23; in a sitting posture, 29; whilst walking two miles an hour, 70·5; in walking three miles an hour, 100·6; and upon the treadwheel lifting his body, 28·65 feet in a minute, as much as 189·6 grammes per hour.

The recent observations of Fick and Wislicenus, on the result of a certain amount of work performed by themselves, also point to the conclusion, that muscular effort, on a *non-nitrogenous* diet, does not increase the quantity of urea excreted from the body; moreover, they conclude that the oxidation of the quantity of albuminoid substance, or plastic nitrogenous material, which would correspond with the urea and other nitrogenous compounds then excreted, does *not* yield sufficient potential energy to perform the work accomplished. The mechanical work undertaken by them, was the ascent of the Faulhorn, a mountain in the Bernese Oberland. From the middle of the day before, until the ascent was completed, no albuminoid food was taken, so that no excess or *luxus consumption*, might interfere with the experiment. During the hours of the night previous to the ascent, the quantities of urea excreted by them respectively, were by Fick, 12·5, and by Wislicenus, 11·7 grammes. During the 7 hours and 40 seconds occupied in the ascent, or *work-hours*, i.e. from 10 min. past 5 A.M. to 20 min. past 1 P.M., the quantities were 7· and 6·7 grammes. During the next 5 hours and 10 min. of rest, or *after work*, in which an abundant meal of meat was consumed, the quantities were 5· and 5·1 grammes. The quantity of urea excreted per hour was, therefore, *not* increased *during exercise on a non-nitrogenous diet*. In determining the relation between the quantity of albuminoid substance decomposed, and the mechanical work performed, they take into account not only the urea, but the whole nitrogen eliminated in a more or less oxidised form, and they find that this, during the actual period of *work*, would represent in F. 22·098, and in W. 20·89 grammes of albumen. The minute trace of nitrogen given off from the skin, is neglected, and so is the larger quantity contained in the feces, because it passes off in almost unoxidised compounds. The possible retention in the system, of some partially oxidised albuminoid substances, such as creatin, is admitted; but to compensate for this, they add a quantity of albumen, equal to the nitrogen excreted in the period of *after work*, making the respective totals, 37·17 and 37 grammes.

albumen oxidised. The heat given out by the oxidation of these quantities in the body, is unknown ; but from avowedly imperfect data, and making the fullest possible allowance, they conclude that the energy obtainable from its oxidation, might be for F. 250,000, and for W. 249,000 heat-units ; giving respectively 106,250, and 105,825 met. kils. of mechanical power. Now the chief work actually performed by them, was lifting the weights of their bodies, as clothed, through the height of the mountain ; this is measurable by multiplying the former by the latter. Thus F. exerted a force of $66 \text{ kil.} \times 1,956 \text{ metres} = 129,096 \text{ met. kils.}$, and W. a force of $76 \text{ kil.} \times 1,956 \text{ metres} = 148,696 \text{ met. kils.}$; if to this, be added the internal work of respiration and circulation, the totals are for F. 159,637, and for W. 184,287 met. kils. These results show, therefore, that the mean work performed, in proportion to the power derivable from the oxidised albumen, was as 3 to 2. It is well known, however, that much other work is performed in the exercised body, which does not contribute directly to the external work performed ; and Heidenhain has computed that only one half of the energy of the force-generating processes, is really used as work. Hence, double the amount of work was actually performed in the bodies of F. and W., or 319,274 and 368,574 met. kils. ; in other words, the ratio of work performed, to the power derivable from the consumption of albuminoid substances in the body, was as 3 to 1. Since, therefore, it is impossible for the oxidised albumen, to be the sole and exclusive source of the power manifested in the work of the body, to which it can contribute so little, they conclude that the oxidation of non-nitrogenous substance, must yield, at least, the larger proportion of the force required, not only for the production of heat, but also of mechanical motion. Moreover, since it is improbable, that, in so delicately an organised apparatus as the muscular tissue, two sorts of decomposition should occur, for the purpose of liberating the same force, they believe that, as non-nitrogenous substances *are* decomposed *for that purpose, those only* are decomposed. The nitrogenous substances of the muscle, however, simultaneously undergo waste or wear, and thus yield urea. In conclusion, they show that the resemblance of the living animal body to a steam-engine, is more close than is usually admitted ; the muscle is an apparatus for burning its appropriate fuel, the hydro-carbons and carbohydrates, in the same manner as an engine burns its proper fuel, coal or coke ; in action, the muscle does not specially oxidise itself, any more than the engine is burnt ; but in action, both the muscle and the engine undergo wear. In use, the wear, in either case, is not much increased, but the consumption of fuel is decidedly greater. It is possible, they remark, either that non-nitrogenous substances in the muscle, act as the combustibles, or that they pass through the muscle in a *rapid stream*, their particles being immediately oxidised, and then carried away.

The general conclusions of Fick and Wislicenus, are strengthened by the subsequent researches of Dr. Frankland, who has also supplied more secure data, for estimating the heat-units produced by the oxidation of albuminoid substances in the body. It was admitted by the German physiologists, that these could not be equal to the heat-units evolved by the combustion of the separate elements of albumen out of the body, although they allowed that quantity in their calculations. By mixing a certain quantity of *muscle* deprived of fat, *albumen*, and *urea*, all dried at

212° F., with chlorate of potash, deflagrating the compounds, and measuring the heat evolved, by its effect in raising the temperature of water, Dr. Frankland shows that 1 gramme of each of these substances respectively evolves, 5,103, 4,998, and 2,206 heat-units. Now, as the muscular substance is imperfectly oxidised in the body, forming urea, or some still less completely oxidised material, it can only yield the above-mentioned number of heat-units, minus the number producible by the quantity of the imperfectly oxidised nitrogenous substances into which it is converted in the system. Albuminoid bodies, in undergoing decomposition, yield about $\frac{1}{3}$ rd their weight of urea. Hence, using the above given data, 1 gramme of dried muscle oxidised in the body, would yield $5103 - \frac{2206}{3}$ or $5103 - 735$ heat-units = 4368 heat-units, or 1848 met. kils. of mechanical power; for 1 gramme of pure albumen, the results are 4263 heat-units, or 1805 met. kils. of force. Applying these data to Fick and Wislicenus' experiments, it will be found that, as they eliminated respectively nitrogen equal to 37.17 grammes, and 37 grammes of albuminoid substance, the available energy they produced would be only 68,690, and 68,376 met. kils.; whilst their computed work was 319,274 and 368,57 met. kils. The mean ratio of the work performed, to the power derivable from the oxidation in the body of the nitrogenous substance of muscle was, therefore, less than they had supposed, viz. as 5 to 1.

Again, if the method devised by Frankland, for measuring the energy derivable from the oxidation of albuminoid substances in the body, be correct, then the determinations of Haughton and Playfair are inadmissible. Moreover, applying the same data to the observation of Edw. Smith on prisoners working on the treadmill, to those of Haughton on men engaged at shot drill, and to those of Playfair on fully employed labourers, Frankland found that the work accomplished was, in the first case, nearly 2 to 1, in the second case, more than 2 to 1, and in the last case, 1.3 to 1, in proportion to the force indicated by the excreted nitrogen; and yet, in each of these cases, unlike the experiments of Fick and Wislicenus on themselves, the food contained a large amount of nitrogenous substances, which increased the quantity of nitrogen eliminated. Fick and Wislicenus intentionally consumed *non-nitrogenous* diet.

Dr. Frankland agrees with the previous conclusions, that the transformation of muscle tissue, is almost entirely independent of the *amount* of work performed; that, in Man, non-nitrogenous substances must be the chief source of the energy which is transformed into muscular work, and that the muscle is an apparatus in which this energy is evolved, at the expense of hydro-carbonaceous fuel, or a machine for converting potential energy into mechanical force, and that it does not undergo much more waste when in action, than when at comparative rest. Besides this, he believes that the oxidisable material does not require to be previously organised or made part of the muscle, but only to be digested and assimilated into the blood, of which it forms a part. He conceives that the materials of the food, together with oxygen, circulate in the blood, going through the muscle, and that when the latter is quiescent, no chemical action takes place; but that when a muscle is excited to action by a nerve, the nerve force determines the oxidation of non-nitrogenous matters in the blood, and so sets free potential energy, partly acting as heat, and partly as motion. Dr. Frankland admits, however, that

nitrogenous matters may also be employed for this purpose, as is illustrated by the work performed by men and animals fed on flesh diet. But ordinary flesh contains much fatty matter.

Dr. Parkes has observed the effects of exercise and rest, under different diets, on the excretion of urea, over longer periods than those noticed by Fick and Wislicenus. His results likewise show, that on a non-nitrogenous diet, exercise produces no increase in the excretion of nitrogen; that less urea is excreted during the period of actual work; and that, the elimination of nitrogen, is regulated, rather by the character of the diet than by the amount of exercise. The subjects of observation were two healthy soldiers, whose normal daily standard of excretion of nitrogen, was first ascertained during a period of six days, in which they took their ordinary food and exercise. For two days, they consumed non-nitrogenous food, and rested; the urea, and the total nitrogen excreted, then fell to a mean of less than one-half the normal quantity, and yet the men lost weight. They next returned for four days, to their ordinary diet and occupation; the nitrogen excreted, as urea and otherwise, immediately increased from day to day, but did not, on the last day, reach its normal standard; and the total quantity excreted in the four days, was less than half of that eliminated in four of the first six days; some nitrogenous food was apparently retained for the nutrition of the tissues, or to supply the nitrogenous blood-material expended in the two days of non-nitrogenous diet. For the next two days, the men again took non-nitrogenous food, but instead of resting, they underwent full exercise, walking, on the first day, 23·76, and on the second, 32·78 miles; the food satisfied the sense of hunger which was felt; much fatigue was experienced, especially on the second day; the excretion of nitrogen *decreased* during the first thirty-six hours, but in the succeeding twelve hours, which were hours of rest, it showed a marked *increase*; the pulmonary and cutaneous excretions increased, the former 100, and the latter 50 per cent.; the men lost weight. Finally, being allowed their usual diet, with ordinary exercise, the quantity of urea again rose daily, and at last surpassed the normal quantity. The chief difference in these results, as compared with those of Fick and Wislicenus, whose observations were not sufficiently prolonged, is in the increased excretion of nitrogen, during the hours of rest, after severe exercise on a non-nitrogenous diet. This may merely show that the effects of the changes taking place in the muscles during exercise, are slow to manifest themselves in the excreta. The diminution in the nitrogenous excretions, during actual work, on a non-nitrogenous diet, may, as Parkes suggests, be owing to nitrogen being then retained and used, and not to the entire absence of nitrogen in the muscular tissues.

In subsequent experiments on this subject, Dr. Parkes found that, upon an ordinary mixed diet, containing a daily quantity of about 19·6 grammes of nitrogen, rather less of that element was excreted during the early periods of exercise, and during actual exercise, than during rest, especially during the rest immediately after work, when the quantity rose, as to be excessive. He suggests a new explanation of the facts, viz. that a muscle increases in size when in action, then appropriating more nitrogen than it loses; but that, when it is at rest, it lessens in bulk, using more nitrogen than it appropriates. Muscular movement is regarded as due to a process of *formation*, and repose as accompanied

by disintegration. The non-nitrogenous substances surrounding the ultimate muscular elements, undergo change during the action of the muscle; the effete products, chiefly of those non-nitrogenous substances as Ranke and others have supposed, arrest the muscular contraction; a period of rest follows, in which the effete products are removed, and nitrogen is eliminated; and the muscle is once more fit for action. This view explains most of the facts very well; it is also in accordance with experience, as to the necessity of nitrogenous food for persons engaged in prolonged muscular work; and yet it admits that the changes in the nitrogenous elements of muscle, are inadequate to produce the movement, and refers these to the chemical energy evolved by some neighbouring non-nitrogenous substances.

The views of Liebig, as to the separate and exclusive source of heat and motion in the animal economy, are, therefore controverted by more recent knowledge; it is certainly disproved, that the disintegration of muscular substance, is the only source of muscular power; and it is equally proved that in Man, and probably in Omnivorous animals, the oxidation of non-nitrogenous materials is its chief source. But the chemical powers of the living animal economy, have perhaps been underrated; and *à priori* theories may, in both directions, limit too much our notions respecting them. Carnivorous animals, as would appear from the observations of Lawes and Gilbert on fattening animals, of Savory and others, upon rats and dogs fed on a flesh diet exclusively, have the power of splitting up albuminoid bodies into fats and certain nitrogenous compounds. If so, this fat on being oxidised, may become the source of motor power. Besides, as albuminoid bodies are undoubtedly oxidised in the body, they must furnish potential energy transformable either into heat or motion. It seems impossible to believe, with Dr. Frankland, that the *blood only*, and not the *nervo-muscular substance* also, is oxidised in the production of muscular force; or to deny that nitrogenous substances may also yield *force*, as well as heat. Work is well performed, for a short time, on a non-nitrogenous diet, but fatigue is at last felt, and nitrogenous matter must be wasted; otherwise it would not be retained in unusual quantity, when nitrogenous food is again taken, after a temporary abstinence from it. Nitrogenous food must therefore be supplied, probably, in accordance with the amount of work done (Parke). A muscle may be a machine, and the blood circulating through it, the fuel; but being a living tissue, it, and its nerves and controlling nervous centres, waste, or they would not become fatigued and exhausted by work. A muscle probably wastes

more than a machine wears. This waste may depend largely on the loss of the hydrocarbons, and carbohydrates, in the muscle, and the nerves, yet the more abundant nitrogenous substances in them must likewise participate in the exhaustive process. Before, too, we accept Dr. Parkes' view as to muscular action being accompanied by an absorption of nitrogenous substance, and by growth, it becomes necessary to determine the amount of brain-, spinal-cord-, and nerve-substance, which is consumed, or changed, in all motor acts. This is probably considerable, and possibly largely affects the *fatty matter* of those organs. Might not this oxidation, together with the nutritive changes accompanying it, explain, in part, the increased evolution of carbonic acid during exercise? By occupying the oxygen in the blood, it might also account for there being less to act upon the *muscular* tissue. Yet, we know nothing of the amount of change in the nervous substance considered separately.

The exact destination of the potential energy, liberated by the double process of oxidation of nitrogenous and non-nitrogenous materials, which undoubtedly takes place in muscular motion, cannot at present be precisely pointed out. In man, the latter substances undergo far more abundant decomposition than the former, and, as remarked by Frankland, whilst the nitrogenous materials are only partially oxidised, being discharged as urea, and retaining about $\frac{1}{4}$ th of their potential energy unexpended, the non-nitrogenous substances yield all their energy in the body, being oxidised perfectly as carbonic acid and water.

There are many facts which indicate the necessity for large amounts of non-nitrogenous food, for the due performance of muscular work. It is in the larval stage, that Insects generally consume the most albuminoid food, and perform the least amount of work, whilst, in the perfect condition, as in bees, butterflies, and moths, their muscular activity is remarkable, though their food is almost purely saccharine or non-nitrogenous (Verloren). The goat, chamois, gazelle, and many other ruminants, are singularly swift and active creatures; their food, however, is not highly nitrogenous, but chiefly consists of carbohydrates. It is not probable that the muscular work in any of these cases, is performed by the oxidation of albuminoid matters only; for, in that event, the muscles, especially the minute ones of Insects, would soon be entirely oxidised, and could not be restored by the scanty supply of nitrogen in

the food. The remarkable provisions for digesting the carbohydrates and rendering them absorbable, appear therefore to have reference, not only to their use as heat-givers, but also as sources of motor power. The production of sugar from starch is a universal action of the saliva of all animals, and long-continued digestion in the Ruminant stomach, will even change the cellulose. It has been remarked, that the chief food-manufactures are concerned with non-nitrogenous articles of diet: that eggs contain, when dried, 40 per cent. of fatty matter; that fat is always present in meat; that the poor consume much bacon-fat; and the rich, who eat most albuminoid food likewise take more butter, sugar, and alcohol (Lawes and Gilbert). The use of bacon by the agricultural labourer has given rise to a familiar epithet for him. The chamois-hunters prefer a store of bacon-fat and sugar, to any other provisions, on a hunting expedition; and Fick and Wislicenus ascended the Faulhorn on non-nitrogenous diet, without special fatigue. But, on the other hand, Parkes found, that on the second day of severe exercise, on a non-nitrogenous diet healthy soldiers complained of unusual fatigue. Practically it would seem that sufficient nitrogenous food being supplied for the nutrition of the muscular and nervous system, then the most effective diet for a labourer, is that which contains a large proportion of non-nitrogenous substances. Athletes should *train* on meat, but enter into their contests, upon amylaceous-saccharine, or fatty food.

Dr. Frankland has extended his method of determining the heat-units by deflagration with chlorate of potash, to various articles of diet, in order to test, in this way, their mechanical equivalents, or *motor values*. The actual energy of a given weight, 1 gramme, of each substance, when burnt out of the body, is ascertained by experiment; and, in the case of albuminoid bodies, the energy which would be developed from them, when oxidised, in the body, is calculated, by deducting the energy remaining in a corresponding quantity of urea. The following Table gives some of the results:

According to this mode of estimating the value of food, compared with that which regards its composition only (p. 115) cheese still retains a very high position, being inferior only to oils, fats, butter, and cocoa nibs. It appears, moreover, that 55 parts of fat are equal to 1.15 of cheese, to 1.3 of pea meal, to 3.5 of lean beef, and to 5 parts of potatoes.

Value of Food as a Source of Motor Power (Frankland).

Article of Food in natural condition	Met. Kils. of Force, from 1 Gramme oxidised in the body	Weight in ozs. required daily, to support the move- ments of respiration and circulation
Cod Liver Oil	3,857	1·5
Beef fat (dry)	3,841	1·5
Butter	3,077	1·8
Cocoa nibs	2,902	1·9
Isinglass (dry)	1,914	—
Cheese (Cheshire)	1,846	3·
Oatmeal	1,665	3·4
Arrowroot	1,657	3·4
Flour	1,627	3·5
Peameal	1,598	3·5
Rice	1,591	3·6
Gelatin (dry)	1,550	3·6
Sugar	1,418	3·9
Egg (yolk)	1,400	3·9
„ (hard-boiled)	966	5·8
Bread-crumbs	910	6·4
Ham, lean (boiled)	711	7·9
Mackerel	683	8·3
Beef (lean)	604	9·3
Veal (lean)	496	11·4
Stout	455	—
Potatoes	422	13·4
Whiting	335	16·8
Bass's Ale	328	—
Apples	273	20·7
Milk	266	21·2
Egg (white)	244	23·1
Carrots	220	25·6
Cabbage	178	31·8

Transformation of Mechanical into Calorific Work in the Body.

Every kind of *internal* work, whether vital, mental, nervo-muscular or mechanical, electric or nutritive, excepting the solvent processes, ultimately passes into heat within the body. The purely *external* mechanical work is thought by some, however, to be an exception; but this is not entirely so; it is only in the case, when motion is communicated to external matter. At

the moment of action of a muscle, indeed, an inverse proportion exists between the work accomplished and the heat produced. A muscle develops more heat, when it cannot shorten itself, so as to produce external movement or work; as, for example, when a person attempts to move an overwhelming weight, or overcome an unyielding resistance, as compared with the effect of free action in lifting a movable weight. Any effort or motion which is stopped or resisted, or which disappears in any way, passes necessarily into heat; even the electric currents in muscles and nerves, when they are lessened by disturbance, or rest, contribute, however slightly, to raise the temperature of an acting muscle, and therefore of the body. In fever, the muscles may become as hot as 105° Fahr., and in tetanus, 111° Fahr. (Ludwig); they are then hotter even than the blood (Fick); but this happens when most of their chemical energy of decomposition can pass into heat, none being required for work. During muscular action, the chemical energy passes into that *perceptible motion*, which we call contraction or shortening; during arrested effort, it appears in the *invisible motion*, which produces heat.

On the supposition, that the muscular force is derived from the oxidation of albuminoid substances, the greater part or the whole of it, is ultimately transformed into heat, and is added to the avowedly larger store derived from the non-nitrogenous food. But the theory which regards animal motion, as chiefly, or entirely, derived from the energy supplied by the non-nitrogenous materials of the blood or tissues, and therefore from the non-nitrogenous food, is not inconsistent with the view, that these latter are the calorific or heat-forming materials; for they then serve both offices. The transformation of potential energy into muscular power, whether exerted internally or externally, is necessarily accompanied by the ultimate production of heat within the body; and this is the chief, and probably the only, source of animal heat (Frankland).

Nutritive or Assimilative Work.

The assimilative work performed in the body, is also chemical being partly liqueficient, partly dialytic, and partly solidificient. It must be performed at the expense of chemical energy developed during the many transformations of the nutritive materials, as these are, in turn, digested, hydrated, dissolved, absorbed, and converted into tissue. The amount of force

employed in digestion, is small, as compared with the other great demands of the system. Playfair suggests that it is measurable, by the amount of nitrogen of the nitrogenous substances found in the solid excreta; and that it may, as he thought of the mechanical work, be ultimately referable to the energy of the albuminoid food. The quantity of nitrogen which escapes by the lungs and skin, is quite unimportant; with ordinary diet, the urea includes $\frac{1}{12}$ ths of that contained in the food, whilst the solid excreta yield about $\frac{1}{12}$ th (Ranke). This small quantity is the residue of the mucus, salivin, pepsin, pancreatin, glycocoll, and taurin of the digestive fluids, the solid constituents of all of which, in a Man, weighing 150 lbs., would be upwards of 8 oz. per diem. Playfair supposes that, whilst most of the substances are reabsorbed, a certain portion of each undergoes chemical change, being, as it were, degraded, and becoming unfit for entering the circulation. This remains, therefore, as a quantitative expression of the force which has been employed in the processes of primary assimilation. It may be a residual index of such actions, but not a source of power itself, for it escapes unoxidised. All nutritive work, implying solidification of material, likewise ultimately passes into heat.

Electrical Work.

The currents of electricity developed in the body generally, those found between arterial and venous blood, in muscle and in nerve, in secreting and in special electric organs, are developed through chemical action, involving waste by oxidation of the blood or tissues, and indirectly therefore of the food, whether of the nitrogenous or non-nitrogenous food, or of both, is not yet determined. They do not appear to be derived from friction, changes of temperature, or magnetism, as in the inorganic world. The chemical energy of the body, thus diverted to electric work, cannot, however, be expressed in numbers. Unless it passes off to surrounding objects or media, it is converted into heat, or into motion and heat, within the frame, and so assists in the calorific work.

Nervous Force and Work.

As elsewhere mentioned (vol. i. p. 284), there exists in nervous substance, a peculiar electro-polar condition of the nervous molecules, which is altered, not merely by the passag-

of an ordinary electric current through a whole nerve, as is the case with the muscular current, but also when that current, or any other stimulus, traverses a small portion of the nerve. The existence of nervous substance, is essential to the manifestation of this peculiar condition ; the force concerned in its production, may be itself what is called the nerve-force, or it may be transformed into that force, serving, in either case, to excite the contraction of a muscle, on the one hand, or the reflex or sensitive excitability of a nervous centre, on the other. The reaction of a reflex nervous centre, may also require, or depend upon, such molecular polarity. Even sensation, and the higher and purely mental processes, are associated with, and rest upon, similar molecular conditions and properties. The special condition of the nervous matter, which accompanies sensation, emotion, thought, consciousness, and will, is unknown to us ; but the molecular polarity of the nerve-substance, is, as much as the nervous substance itself, a part of the constitution of the living animal body. The polar condition of the nervous molecules, represents a portion of the vito-physical work of the system ; and variations in it, are associated with changes in the nervous matter itself. These changes are chemical, and imply waste, oxidation, and renovation. All nervous action, or work, requires both food and air, containing stores of force, which, exhibiting itself first in chemical combination, is transformed into the electro-polarity proper to, and manifested only by the nervous substance built up within the bodies of animals, and capable of being excited by appropriate stimuli.

The portion of nervous work, performed in the control of the various muscular acts, voluntary or involuntary, and belonging to the animal or vegetative functions, cannot, at present, be dissociated, in any calculations, from the muscular work itself. As to the nervous work connected with sensation and other psychical actions and reactions unaccompanied by motor results, it is impossible, at present, to measure them, and Haughton's allotment of the so-called *mental work* of the body, to a certain proportion of the urea, is purely conjectural. It is not even known how far it may be due to changes in nitrogenous or non-nitrogenous matter ; it probably depends upon both. Possibly some estimate of its amount, might be made, by studying the amount and the sources of the phosphates formed in the system. Urea is probably produced by the decomposition of nervous substance, especially of the albuminoid axial fibres, and non-medullated terminal portions of the motor nerves ; urea ha:

been found in the muscles of certain Fishes. The phosphates of the juice of muscle, and the phosphorus in the red corpuscles of the blood, may be a source of phosphates in the urine; but the cerebrie acid of the grey nervous substance, is especially characterised by containing phosphorus, probably unoxidised; and over-activity and disease of the nervous system, are said to increase the amount of phosphates so excreted. The oxidation of phosphorus, or of phosphuretted fat, may be one source of electro-polar nerve-force. In any case, such molecular polarity is ultimately transformed into heat within the body, and affords another example of the economy with which the various forms of vito-physical force engendered in the animal system, are employed within it. The energy of every substance oxidised in the body, into whatever form of force it may be transmuted, is doubtless applied with the least possible loss.

In conclusion, it may be observed that, although the results of the application of the principles of physical research, to the explanation of the physiological phenomena discussed in this Section, are at present incomplete, yet, considering the extreme complexity of the phenomena exhibited by living animals, and the difficulty, even in regard to Man alone, of obtaining correct average numerical data, enough has been determined to render it certain, that all the strictly physical processes within the body, whether chemical, mechanical, thermic, electric, or photic, are performed by modifications of the common force which produces similar phenomena in the inorganic world around us.

There exists, however, in the living animal, as in the living vegetable organism, a special *formative* or *organising* energy, evolving the perfect animal or plant from the primitive ovum or ovule, developing its various tissues and organs, and conserving these from the commencement to the termination of its individual existence. The influence of this force, moreover, extends from the parent to the offspring, generation after generation. Its relations to the vito-physical and vito-chemical forms of force working in the body, are entirely unknown. Its truly marvellous results are considered in the following Section on Reproduction Development.

REPRODUCTION.

Spontaneous Generation.

THE life of individual organisms, whether vegetable or animal, is limited, death, at last, ensuing from accident, disease, or natural causes. The maintenance of the species, by the reproduction of new individuals, is accomplished in different modes in different animals.

All animals, so far as is known, even the very lowest, are produced from *parents*. The occurrence of the original generation of an animal, without the intervention of a parent, or the so-called *equivocal* or *spontaneous generation*, is not believed in by the best authorities. All cases of supposed spontaneous generation, cited before the introduction of good microscopes, may be set aside as valueless. The present condition of the question, is fully illustrated in the recent controversy between MM. Pouchet and Pasteur. It is admitted by both those observers, that only the lowest Protozoic forms of animal life are concerned in this question, the assertions of Crosse and others, as to the spontaneous development of a complete Annulose animal, being unworthy of serious consideration.

With regard to the Infusoria, however, it is alleged by Pouchet, that, if impure water be boiled, so as to destroy all organic life in it, and then be absolutely excluded from the air; or if air only be admitted which has previously passed through red-hot tubes; or, again, if water be boiled in flasks which are then hermetically sealed—organisms, belonging to the simplest forms of Infusorial life, will make their appearance; and that these will even be followed by the subsequent appearance of higher ciliated Infusoria. It is strongly asserted that, in such experiments, absolute care has been taken to prevent the accidental intrusion of germs, however minute, into the water or air. By Pasteur, on the other hand, it is affirmed that, if sufficient precaution be taken, no manifestation of life occurs in the fluid experimented upon, or, at least, so exceptionally, that it may well be attributed to the accidental entrance of floating germs.

The following experiments have been devised by Pasteur, to illustrate this subject. Small flasks of boiled water, have been closely fitted, at the mouth, with tubes, into a bend or bulb of which, cotton-wool is introduced; this intercepts floating germs, but yet allows the interchanges proper to

gaseous diffusion: in such experiments, no organisms are developed in the water. On the other hand, with the same fluid boiled, and placed in a flask, fitted with a similar tube without the cotton-wool, multitudes of Infusoria are developed. In other experiments, instead of cotton-wool, gun-cotton was employed, and placed so as to intercept the germs in the air; this gun-cotton being afterwards dissolved in ether, ova, and germ-forms were collected in the residue, and recognised under the microscope. Moreover, portions of the cotton-wool or gun-cotton charged with the germs, produced, in water or in vegetable infusions, the same kinds of Infusoria as appeared in the liquids unprotected by the gun-cotton.

It would seem, however, that in boiled vegetable infusions, hermetically sealed with a certain quantity of air, also previously heated to a red heat, those singular organisms, named *bacteria*, which are probably vegetable, may, after *several months, appear* (Child).

The position of the advocates of the doctrine of spontaneous generation, is a difficult one. An apparently positive result, in an experiment with hermetically-closed vessels, is attributed by their opponents, to want of care in the preparation of the water or the infusion, or to the accidental intrusion of germs. The position of the opponents of the doctrine, is also difficult, because they seek only to establish a negative. A sufficient number of *negative* results, obtained by conscientious observers, is all the evidence that can possibly be advanced in such a case. The *onus probandi* is thrown upon the supporters of the doctrine.

The Various Modes of Reproduction.

In the Vegetable Kingdom, two modes of reproduction are observed, viz. the *nonsexual* and the *sexual*. The former presents several varieties, viz. *gemination*, or the formation of *buds*, as in ordinary plants, or in special cases, of *bulbs* which are detached buds, or *subdivision* or *fission*, as in the microscopic algæ, and perhaps in the lower fungi. The sexual mode is by true *spores* or *seeds*, which require fertilisation. The two modes commonly occur in all plants.

The mode of propagation by *buds*, or by *cuttings*, serves to prolong a variety, or a species, merely by multiplying the individual; but the *sexual* mode alone will render permanent an accidental variety, or will perpetuate, for a length of time, a specific form. In the fungi, and in the lower algaecious forms, it seems probable that an *alternate form of generation* may occur, such as will presently be described, in the case of

certain animals: that is to say, the two forms of reproduction, *sexual* and *nonsexual*, may alternate in different generations; in other words, spores may produce intermediate forms, which, in their turn, may directly reproduce the parent form.

The reproduction of *animals* from parents, also presents the *nonsexual* and the *sexual* modes.

The *nonsexual* mode of reproduction, may either consist in a simple cleavage or division called *fission*, or in the formation of *buds*, known as *gemmation* or *budding*. Both these forms occur only in the lower Classes of animals. *Fission*, or *fissiparous reproduction*, consists of a constriction, once or several times repeated, in the soft body of an animal, followed by its complete division into two or more parts, each of which is then developed into an individual as complete, in every respect, as the parent animal. This form of reproduction is noticed as one mode of development in the Infusorial animalcules, the process being sometimes, as in *Paramecium*, extraordinarily rapid. It also occurs in the formation of the segments in some vermiform intestinal Entozoa, but not amongst animals higher in the scale. In artificial fission, as performed upon the *Hydra*, a similar process is imitated. If, for example, a *Hydra* be cut, lengthwise or transversely, into several parts, each portion will complete itself. Some of the Annelida, or Worms, on being cut across, develop a new head to the lower half, and a new tail to the upper portion, of the divided body.

Gemmation, or *gemmiparous reproduction*, consists in the formation of an offshoot or *bud*, from the body of the parent animal, which either continues to grow in connection with the parent, so that composite animals are produced, as the many-chambered Rhizopods; or aggregates or *colonies* of animals are formed, attached by a common stem, or *stolon*, as in the case of the Vorticellæ, amongst the Infusoria. This is, also, the ordinary mode of propagation of the *Hydra*, amongst the Cœlenterata; of the compound coralline Polyps, of the compound Ascidioida, and of *Nais*, amongst the Annelida. Gemmæ may also, after a time, detach themselves from the parent stem, move away, and develop as independent animals, which may themselves gemmate, and form a new colony, as in the compound Polyps and the compound Tunicata, or become new independent animals, as in the Medusæ. Sponges are thus reproduced by detached bodies, known as *gemmules*, which, at first ciliated and free-moving, afterwards become smooth and fixed, and then grow into a new sponge.

As representing a special form of *internal gemmiparous* reproduction, may perhaps be included those remarkable cases, in which groups of minute cell-like bodies, sometimes named *pseudova*, to distinguish them from *true ova* or *eggs*, are developed somewhere in the interior of the body of the parent animal, and, after a time, undergo successive stages of development, sometimes into forms externally resembling that of the parent animal, though not possessing reproductive organs, but much more commonly into forms not resembling the parent animal. By detachment, protrusion, or rupture of the parent, these new animals then become independent beings. This form of reproduction is observed in the Aphides only, among Insects, and in the Daphnia, among the smaller Crustacea. Light and heat are important agents in determining the occurrence of this process.

The larger reproductive bodies found in the Sponges, and developed as cold weather approaches, called *capsules*, have by some, been regarded as of the nature of *pseudova*, but they may be *sexual* products. The so-called *germ-cells* of the Hydra, which, towards winter, are sometimes developed in the walls of the gastric cavity in one individual, whilst a *sperm-cell* appears in that of another, though sometimes both kinds of cells are developed in the same Polyp, have likewise been referred to this class of bodies; but their *sexual* character is more probable.

In the *sexual* mode of reproduction, known as *oviparous reproduction*, which is a higher form of propagation, an *ovum*, or *germ-cell*, and a *fertilising cell*, or *sperm-cell*, are always necessary, and co-operative, in other words, a *female* and a *male* product, according to the distinction of *sex*.

In some animals, as in the Cœlenterata, in certain Scolecida, as in trematode Entozoa, in many Gasteropods, and in a few branchiated Annelida, the male and female products are developed in one individual, which is then said to be *monœcious* or *hermaphrodite*. In the Medusæ, and in the Entozoa, the germ-cells are fertilised by the sperm-cells of the same animal; but in the Snails, and other Pulmo-gasteropods, there is an interchange of office, one individual fertilising the ova of another, and having its own ova fertilised in return.

In the remaining animals reproduced by true ova, viz. the higher Annuloida and the Annulosa, the Molluscoida, Mollusca, and Vertebrata, the reproductive elements are found in separate individuals belonging to opposite sexes. Such animals

are named *diœcious*. The ovum is then, in some cases, as in Fishes and Amphibia, fertilised without, but in other cases, as in Reptiles, Birds, and Mammalia, within, the body of the female or ovigerous parent. In this ovum, when fertilised, the embryo is developed, undergoing a series of important changes, which constitute the process of *evolution* or *transformation*.

Some curious examples of the *coexistence in the same individual*, but at different seasons, of a *sexual* with an apparently *nonsexual* mode of reproduction, have been met with, in the lower Classes of animals. This presents us with the various forms of *parthenogenesis*, or *development* by so-called *unfertilised ova*. This mode of reproduction, is illustrated in the Aphis, amongst Insects, in the female of which, one act of fertilisation is sufficient for a long succession of distinct reproductive acts. Another most striking example is exhibited by the Bee, as was first observed by Dzierson, and afterwards by Siebold, Berlebach, Leuckart, Owen, and others. The ova of the Queen-bee are deposited by her, in the cells of the comb, and in that act, according to the size and form of the cell, she either fertilises the ovum, or not. This is accomplished by her permitting, or preventing, the escape of a small quantity of fluid from a sac in the interior of her body, named the *spermotheca*, which has been previously charged, by the act of the male bee, with fertilising fluid, during flight in the air. If the ovum be fertilised, it produces a working-bee, *i.e.* an undeveloped female, any one of which, by abundance of feeding, may become a queen-bee. But if the ovum be not fertilised by the fluid of the spermotheca, it produces only a drone, or male. This latter result may be brought about experimentally, either by interruption of the communication between the spermotheca and the oviduct, or by the effects of a temperature low enough to destroy the properties of the fertilising fluid. So also, if the wings of the queen-bee be cut, she remains with the sac uncharged with the fertilising fluid, and her eggs, which she will then deposit all the same, produce only drones. Moreover, a working-bee, not fed up to the condition of a queen-bee, may deposit eggs, which, not having been fertilised in the ordinary way, produce only drones. In the Bee, therefore, the phenomenon occurs, of an ovum undergoing development, without obvious direct fertilisation. Hence the name *parthenogenesis*. Similar phenomena have now been observed in many other Insects.

In certain remarkable cases, a sexual generation by *true*

fertilised ova, or *germ-cells*, may occur, together with reproduction, by apparently *unfertilised pseudova*, or *germinal cells*. This happens, for example, in certain Entozoa, and also in the Aphids, or plant-louse. Sometimes these two modes of reproduction *alternate*, in *different generations*, more or less regularly. In such cases, the form of the animals produced from the *true ova*, or the *first* generation, differs, in some respects, from that of the parent, especially in being nonsexual; whilst the offspring of these, or the *second* generation, derived from *pseudova*, may either resemble the original parents, or may produce, *nonsexually*, a *third* generation, or *several* generations, the last of these producing animals, which are sexual and resemble the parents. This is named propagation by *alternate generation*. In it, a female parent animal produces *ova*, which are duly fertilised. The embryos, or *larvæ*, developed from these, are, at no time, like the mother; they grow, and then develop, in their interior, either a single individual, which becomes like the parent; or they may, by external division, or external or internal gemmation, produce any such; or they may form, either at once, or in succession, a series of young, derived from unfertilised *pseudova*, which, once, or after two, three, or even more generations, ultimately produce animals similar to the first parents. These, again, like those parents, propagate sexually. The intermediate generation, or generations, of *nonsexual proliferous larvæ*, have been called, by Steenstrup, *nurses*, to distinguish them from *true mothers*.

This development by alternate generation, never occurs in the Vertebrata, and only rarely in the higher Non-vertebrata. Amongst the *Mollusca*, no proper example of alternate generation has yet been met with; but it is almost constant in the *Molluscoida*. Amongst the *Arthropodous Annulosa*, it has been observed in but one Crustacean, *Daphnia*, and in only a few Insects, such as the Aphides, but not in the Arachnida or Myriapoda. The Aphides present a remarkable example of this alternation: in the hot season, they multiply rapidly, by successions of internal generations of *pseudova*; but as the temperature is lowered in the autumn, males and females appear, and development by *ova* ensues. In early spring, these *ova* again produce viviparous individuals, which multiply by *pseudova*, and, after many generations, towards the approach of winter, sexual Aphides once more appear. This alternate generation likewise occurs in many Annelida, its

asexual phase then constituting the so-called *fission*, as Nemertes, Nais, and others. It is common also, and occurs in all degrees, in the Annuloida, as in the Scolecide, the Trematode, and the Cestode parasitic worms, in the Rotifera, and the Echinodermata, and also, generally, in the Cœlenterata and in many Protozoa. Amongst the Cœlenterata, and other the form which is evolved from the *fertilised* ovum, is named a *scolex*; the compound forms arising from the budding or fission of the scolex, are named *strobila*, and the perfect animal again exhibiting true reproductive organs, are named *proglottides*. In the Sponges, sexual reproductive organs have been seen, giving rise to bodies like ova, in which a spongilla developed. These alternate with the gemmules. In the unicellular Protozoon, besides fission, the so-called *nucleus* and *nucleolus*, or double nuclei, are believed respectively to represent the *male* and *female* products, not germ- and sperm-cells but germ- and sperm-nuclei.

This mode of reproduction by alternate generation, often presents examples of *genetically-related* animal forms, exhibiting not only a nonsexual character, but a totally different shape and organisation, as compared with the parents. The ovum of certain Echinodermata, of the Echinida and Ophiuri for example, develops into a free-swimming *ciliated embryo*, which becomes converted into a *medusa-like larva*, known as the *pluteus*, a form which has quite a Cœlenterate type; but the body of this, near the digestive cavity, close upon the remaining substance of the original ovum, or yolk-mass, a young *Echinus* appears, in the form of a circular *disc*, which gradually assumes a *quinary radiated* form, and ultimately becomes a perfect Echinoderm. In the same way, the ova of the Tænia or Tapeworms, taken by animals which live upon offal, and swallowed by Man in water, pass into the alimentary canal and there develop into *Echinococci*, or *Cysticerci*, which penetrate, whilst very minute, the surrounding tissues, by a process of boring, and so find their way into all parts of the body and there grow as Cysticerci or Echinococci. The tissues of an edible animal (as a pig, for example), thus infested, being then eaten, the Echinococci, if not destroyed by the cooking, attach themselves to the intestinal mucous membrane of the person who eats them, and form the *head of a tænia*, which then, by successive fission, produces its long segmented body, each section of which, now named a *proglottis*, is really independent of the rest, and is provided with true reproductive

organs, sperm-cells, and ova. The Trichina is not, as was once supposed, an intermediate form, by alternate generation.

Lastly, in the interior of certain Trematode worms, such as the Planariæ, and Distomata, a succession of nonsexual larvæ developed, each producing others within them, until, at last, sexual forms appear resembling the original parent. Thus a Distoma, for example, which is found as an entozoary parasite in the Limnæus, a freshwater snail, develops ova, which are hatched into elongated larvæ of very simple organisation; these larvæ are composed simply of nucleated cells, which grow into ciliated organisms, and then burst through the skin of the larva, attach themselves to a Limnæus, and, having become metamorphosed into a true Distoma, perforate the tissues of the snail.

In these cases of alternate generation, there occurs, therefore, a *sort of metamorphosis*, because the *cycle of evolution* is at last always completed, by a return to the parent form; but the stages of the metamorphosis supervene in *different generations*, and not in the same individual. So likewise, in all cases of *nonsexual* reproduction, whether by so-called fission, or gemmation, external or internal, or by recognised pseudogamy, a return, at last, takes place to sexual development, by the production of ova which require fertilisation. Hence the latter mode of reproduction appears the more important function, to which is assigned the continuance of the *specific forms* of animal life.

In the Molluscoid Tunicata, however, and in Insects, Crustacea, and certain Fishes, and also in Amphibia, a true *metamorphosis* occurs in each single individual—*i.e.*, a transformation takes place not in the embryo *in ovo*, but after the escape of the young from the ovum as an independent being.

In such instances, the young animal, on emerging from a fertilised ovum, has at first no resemblance to the parent, but exhibits a provisional form and organisation, suited to its conditions of life. After a time, however, it undergoes changes; some organs or parts disappear, whilst others begin to be formed, and, finally, it assumes a state of mature existence, resembling its parent, and exhibiting one or other form of sex. Thus the *larva*, or wormlike *caterpillar*, of the Insect, proceeds from the *egg*. Consuming large quantities of food, it grows, and then changes into the *pupa*, or *chrysalis*; in this condition, no food being taken, remarkable changes occur, of which the formation of wings is the most obvious. From

this, finally, it emerges as the *imago* or *perfect* insect. The relative degree or extent of the metamorphosis, differs different Orders and Families of Insects. The suspension or arrest of the ordinary phases of this metamorphosis, occasionally gives rise to monstrosities, such as butterflies with caterpillars' heads, and other curious forms.

Metamorphosis may also be said to occur in some of the lowest Fishes, certain forms of Ammocete having been shown to be the larvæ of the lamprey, which afterwards undergo comparatively slight changes in the buccal and branchial apparatus.

In the Amphibia, the tadpoles of the frogs and others, developed from the egg, present a fishlike form, and possess at first external and then internal gills; but ultimately, in the higher forms, they assume the perfect Batrachian conformation, lose their gills, and breathe by lungs. The extent of change is most marked in the anurous or tail-less Amphibia. In the salamanders, however, no internal gills are developed, like those of the frog; and the tail, instead of undergoing intestinal absorption, is retained. The suspension of the metamorphic process, at certain early stages, leads to the formation of the Perennibranchiate Amphibia, in which lungs also exist, such as the Proteus, Siren, Axolotl, and Menobranchus.

The preceding cases are instances of *progressive* metamorphoses. But metamorphosis may be, as far as general organization is concerned, *retrograde*, animals being, in the larval stage, actively locomotive, and, in the perfect stage, fixed and sessile. Thus, the young of the Ascidioida are free-swimming, tailed, and ciliated animals, whilst in their perfect condition they are fixed. In the Crustacea, the larvæ exhibit progressive metamorphoses of a remarkable character. In the Cirrhopoda, the larvæ are active, move freely in the water, and possess eyes, but, afterwards, they become sessile, fixed by the head, and lose those organs. They present an example of retrograde or recurrent metamorphosis. In the parasitical Crustacea, Lernæada, which attach themselves to fishes, and even in the Lamellibranchiate Mollusca, the perfect animal is less highly endowed than when in its larval condition.

The phenomena of *individual metamorphosis*, so obvious in the Insects and the Amphibia, after their escape from the egg, are, in reality, not singular; for *phases of evolution*, or *transformation*, occur in the development of the embryos of all animals, even of the highest Vertebrata; but these are oft-

mes *rapid*, and occur in such an early stage of embryonic life, as not to be so obvious.

Ova and Pseudova.—A *true ovum*, the product of a female gamete or *ovary*, is a *nucleated cell*, possessing a delicate cell-wall, a contained nucleus, within which is a nucleolus, and, besides that, certain cell-contents. It is a proper and special *germ-cell*, set apart for the reproduction of a new individual.

The male product, or fertilising element, the product of the so-called *sperm-cells*, formed in the testes, is a fluid containing microscopic bodies named *spermatozoa*; these are endowed with the power of active movement, which lasts, in the Warm-blooded Vertebrata, for a few minutes, in the Cold-blooded fishes, for days, and in certain Mollusca and Annulosa, even for months, when received into the special receptacle, or *spermatheca*. From their mode of development, from the character of their movements, and from the effects of reagents upon them, they may be regarded as ciliated gymnoplasmids, or ciliated nuclei, which may be compared to single particles of ciliated epithelium. The sperm-cell in which they have their origin, and from which they escape, by rupture of the cell-wall, is the homologue of the germ-cell, or ovum.

In *true sexual* reproduction, the product of the sperm-cell enters and fertilises the germ-cell, and imparts to it the power of specific reproduction, just as the pollen of the anther of a flowering plant, fertilises the vegetable ovule.

The *unfertilised ovum* of a queen or female bee, and also the *pseudova* of the Aphis, and of other animals propagated by alternate generation, are also *nucleated cells*, portions of the parent animal, set apart for particular purposes, and retaining special powers of further evolution; they are, therefore, also *germ-cells*, or rather *germinal cells*. They may be viewed as undeveloped, or ametamorphosed, portions of a previously fertilised blastema, which has itself resulted from the first stages of evolution of a true ovum; they are, however, retained in connection with some portion, usually internal, of the parent animal, and only indirectly fertilised, offspring, waiting for their opportunity of individual evolution. They have, in truth, *been* fertilised. According to this view, every individual animal form, whether the result of direct sexual evolution, of parthenogenesis, or of any stage of alternate generation, is produced from a primitive cell, which, having been directly or indirectly fertilised, undergoes multiplication and differentiation, so as to evolve the future animal. The simplest forms

of reproduction, by gemmation or by cleavage, are but extensions of individual animals, themselves traceable to the evolution of two primitive, sexually developed, fertilising, and fertilised cells. Even in the lowest Protozoa, evolutions of new beings, from time to time, occur by the conjugation of two nuclear particles in their interior, which, at least, imitate a sexual process.

Whatever variety the reproductive process of animals may present, the primitive cell, whether it be a *fertilised ovum*, an *unfertilised ovum*, a *pseudovum*, or the commencement of a *bud*, is, in all known cases, a part or product of a *pre-existing parent*. No satisfactory proof has yet been adduced, of the *spontaneous* origin of such a cell. Hence the doctrine of spontaneous generation, collapses from failure of proof.

The Ovum considered generally.

The parts seen in an *unfertilised animal ovum*, as already stated, are the cell-wall, the contents, the nucleus, and the contained nucleolus, fig. 116. The delicate *cell-wall* constitutes the *vitelline membrane*, or *yolk-sac*. The more or less transparent granular, or coloured *contents*, constitute the *yolk*. The *nucleus* is a transparent, solid, or vesicular body, here named the *germinal vesicle*, or *vesicle of Purkinje*. Lastly, the *nucleolus* within it, is a fine granular or vesicular corpuscle, called the *germinal spot*. The germinal vesicle and spot are the essential parts, or active centres of growth, of the ovum.

As to the Vegetable Kingdom, in the higher plants, which are produced from seeds, a part exists in the seed, known as the *ovule*; within this which is a vegetable cell, is found the *germ-vesicle*, a structure homologous with the germinal vesicle of the animal ovum. Like it, its future development requires the co-operation of a fertilising agent, which is here derived from the *pollen-cells*. In the lower or flowerless plants, the spores are usually fertilised by *moveable filaments* named *zoosperms*, or by simpler elements.

The *size* of the ovum of different animals, differs very much, not in accordance with the size of the parent animal, but rather with the course and conditions of development of the future embryo. The difference in size, depends almost entirely upon the quantity of the yolk or cell-contents. The character of this yolk also varies; sometimes it is so finely granular and colourless, as to appear clear; whilst, in other cases, it is so distinctly granular and coloured, as to contain large granules and even vesicles, with oil-globules, to 1

ore or less opaque, and to present a pale or deep yellowish
ie.

The *yolk* is a most important constituent of the ovum. In all
ses, it is *formative*, yielding material for the first formation of
e embryo; sometimes it is also *nutritive*, or provides nourish-
ent for it, during a considerable period of its growth.

In one series of animals, *oviparous*, the development of the
embryo within the ovum, occurs entirely after the latter has
en deposited by the parent animal; whereas, in another
ries, often *viviparous*, the embryo is more or less developed
thin the parent. In the *first* case, nutrient material must
specially provided in the ovum, for the future embryo, the
rious organs of which are developed at the expense of the
olk-contents, until the young animal has reached a phase of
velopment, in which it can take external materials for its
ture nourishment. In such cases, the yolk is comparatively
ge in quantity, and rich in organic granular contents, opaque,
d coloured; it is chiefly *nutritive*, and, in small part only,
formative. Such ova are named *meroblastic* (μέρο, a part,
αστός, a germ); they include the eggs of the higher Crus-
tea and Arachnida, those of the Cephalopods, and those of
the Osseous and Plagiostomatous Fishes, of Reptiles and Birds,
and of the Monotrematous order of the Mammalia. The ova
of the Amphibia, are imperfectly meroblastic. In the *second*
case, either a very slight part, or no portion, of the yolk is
nutritive, but all, or almost all, is directly formative; the yolk
is comparatively small, frequently clear, and less rich in gra-
nular organic contents. These ova are called *holoblastic* (ὅλος,
the whole). They are met with in the eggs of the Echino-
dermata and of the Annelids, in those of the simplest Crus-
tea and Arachnida, in those of Insects, and of the Mollusca
generally (excepting the Cephalopods), in the Cyclostomatous
fishes, and, lastly, in the Mammalia, including Man.

The *holoblastic* ovum (fig. 116) consists of a transparent,
homogeneous, or structureless vitelline membrane, which, to-
gether with a clear outer stratum of the yolk, sometimes of
considerable proportionate thickness, constitutes the *zona pellu-
ca*. Within this, and completely filling it, is the limpid, or
fatty granular, germ-yolk, or formative yolk, with its germinal
vicle, and spot. The *meroblastic* ovum (fig. 119) consists, ex-
ternally, of the vitelline or vitellary membrane, which is thin,
and often also homogeneous or structureless, but, in some cases,
slightly granular, or, in parts, indistinctly fibrous. There is

no *zona pellucida*, but the interior of the vitelline membrane is lined with a stratum of polygonal nucleated cells, known as the *epithelial layer*. Within this, is the distinctly granular, nutritive yolk, *a*, which may either be whitish or yellowish. On one part of the surface of the nutritive yolk, is a small circular disc, known as the *cicatricula*, or *germinal disc*. This is, in fact, the *germ-yolk*, or *formative yolk*, spread out, in the meroblastic ovum, upon a small part of the surface of the nutritive or *food-yolk*, instead of being spherical, and occupying the entire vitelline cavity, as in the holoblastic ovum. Lying, at one time, in the midst of the formative or germ-yolk, or germinal disc, are found, as in the other ova, the germinal vesicle and spot (fig. 117).

Fig. 116.

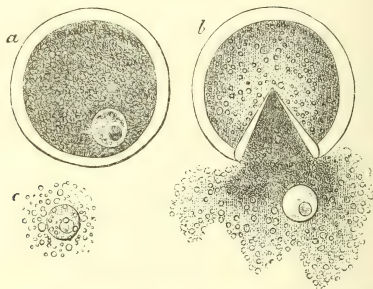


Fig. 116. Holoblastic ovum or germ-cell, of a Mammalian animal, unfertilised (Allen Thomson). *a*, vitelline membrane or envelope, thick, and clear, afterwards forming the *zona pellucida*; within it, is the granular yolk, or cell-contents; in this, the germinal vesicle, or nucleus; and in this, the germinal spot, or nucleolus. *b*, the ovum, or germ-cell, burst, part of the granular yolk, with the germinal vesicle and its contained germinal spot, having escaped. *c*, the germinal vesicle surrounded by a little granular matter.—Magnified 80 diameters.

In the Mammalia, the yolk is so small in quantity, as quickly to become insufficient for the nourishment of the embryo, and special structures are very early formed, to enable it to derive support from the nutrient fluids of the parent. These are imperfectly developed in the Implacental, but are more complete in the Placental, Mammalia. Of the meroblastic ovum, those of Reptiles and Birds, but particularly the latter, present by far the most abundant nutritive yolk. From the size of the egg, and from the occurrence of all the stages of development during an external incubating process, which

may be carried on by artificial means, the egg of the Bird especially presents the most favourable opportunity of watching, from hour to hour, the stages of development of the Vertebrate embryo, within the ovum.

The Ovaries and Ova of the Bird.

The *egg* of the common fowl is first formed within the body of the hen, in the organ named the *ovary*, which is attached to the back of the abdominal cavity, in the lumbar region. In the female embryo of all Birds, two ovaries exist, but almost universally the left one only is present in the mature Bird; the Dorking fowl is an exception, having both ovaries persistent. This is also the case in certain of the birds of prey. The ovary itself consists of a cluster of small spherical bodies, closely invested by membranous *ovisacs*, and named the *ova*. These are at first destitute of the white, and consist only of minute yolks invested with the vitelline membrane. The ovisacs are all held together by a loose areolar stroma and bloodvessels, so as to form a bunch or raceme, and are invested by the peritonæum. To the lower part of the ovary, is attached the wide funnel-shaped opening, or *infundibulum*, and a long tortuous tube, named the *oviduct*, which is also single, being present only on the left side; it opens below into the *cloaca*, or common outlet of the alimentary, urinary, and reproductive organs in the Bird. In the ovary, each yolk is enclosed in its ovisac, the narrow suspensory part of which is named the *pedicle*. The yolks are of all sizes, from that of a pin's head, or smaller, to the completely-formed yolk. In structure, the minute ova at first resemble the holoblastic ova; but as they grow, they become meroblastic, and the *cicatrice*, or *disc* (fig. 117) of the *germ-yolk*, or *formative yolk*, is very early recognised upon the rapidly increasing formative yolk; it is nearly always at that part of the yolk which corresponds with the pedicle of the ovisac. It is now that the *germinal vesicle*, *c, g*, with its contained spot, or *macula germinativa* of Purkinje, are distinctly seen; but no nucleated cells exist. The vesicle and spot disappear as the yolk descends along the oviduct, whether the egg be fertilised or not; they are not found when the egg is laid, fig. 118, but the cicatrice has then become subdivided into two layers, the deeper one containing nucleated cells, many of which are also seen in the central parts of the yolk. As each yolk enlarges, its ovisac increases in vascularity, and, when the yolk approaches maturity, a non-vascular band,

or *zone*, forms around it, in which, at a part named the *stigma*, a rupture occurs, and the yolk escapes into the infundibulum of the oviduct. The remainder of the ruptured ovisac, with its coverings, is cup-shaped, and forms the *calyx*, which gradually shrinks, appearing for a time as a cup-shaped body. As the yolk descends along the oviduct, the mucous membrane of this canal, which is vascular and glandular, secretes the *albumen*, or *white*; this is now added to the surface of the yolk being deposited in spirally-arranged layers, owing to the rotation of the ovum during its descent, in which it is guided by numerous spiral folds of the mucous membrane. The first inner layers of the white, are the densest, and at each end

Fig. 117.

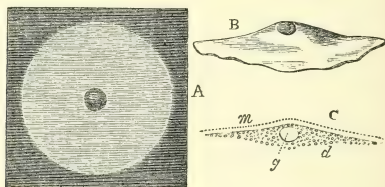


Fig. 117. Part of the yolk of the hen's egg, supposed to be taken from the ovary (Allen Thomson). A, portion of the surface of the yolk, showing the cicatricle, vitelline disc, or germ-yolk, with the germinal vesicle, still present in its centre. (Magnified 6 diameters.) B, side view of cicatricle. C, vertical sectional plan of cicatricle; *m*, vitelline membrane; *d*, granular substance of disc; *g*, germinal vesicle.

poles, are denser and semi-opaque, twisted portions of the white, named the *chalazæ*; the turns of these are in opposite directions, and are also produced by the spiral movements of the yolk, in its descent. Towards the lower part of the oviduct the egg, now composed of the yolk and white, enters a dilated portion known as the *isthmus* of the oviduct, which is lined with a thick mucous membrane, provided with innumerable villi; it is here that the egg acquires a covering, which corresponds with the *chorion* of the Mammalian ovum, and becomes partially calcified to form the shell. The inner part forms the *shell membrane*, and the outer part, becoming calcified, is the *shell*. These being secreted and deposited outside the white, the egg is completed, and then passes through the cloaca to be deposited. Birds are called *oviparous* animals.

The *shell* of the perfect egg (fig. 119, *e*) is composed of 96 parts of carbonate of lime, 2 of phosphate of lime, and 2 of animal matter. The earthy matter is deposited in minute crystalline particles, embedded in a delicate animal basis; the shell is porous, admitting the evaporation of fluid from within, and the passage of gaseous matters in both directions. The *shell-membrane*, *d*, next within the shell, has the appearance of tissue-paper, and consists of several layers of fine matted fibres, running spirally,

Fig. 118.

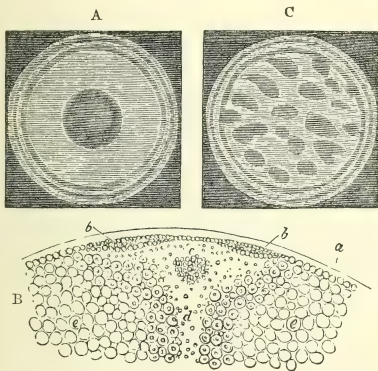


Fig. 118. Cicatrícula of the hen's egg, after it has been laid (Allen Thomson). *A*, cicatrícula, or germ-yolk in a fertilised egg; it shows a transparent central area, looking dark, and a few haloes or haloes near the circumference. *B*, vertical sectional plan of the cicatrícula and adjacent part of yolk, in a fertilised laid egg; *a*, vitelline membrane; *b, b*, thick part of cicatrícula or germ-yolk, with thin part or area in the centre; *c*, group of granules, occupying the position of the former germinal vesicle, which has disappeared in the progress of evolution; *d*, the canal containing white yolk, leading to the latebra; *ee*, the yellow, or nutritive yolk. *C*, cicatrícula of an unfertilised egg; it has no germinal vesicle, and no transparent area, but only irregular blotches.

and composed, it is said, of solidified albumen. At the larger end of the egg, the shell-membrane separates, after a time, into two layers, between which, from the wasting of the fluid of the egg, air finds its way from without through the shell; the interval is named the *air-space*, *f*; it increases with the length of time that the egg is kept; it is not essential to, though it

may assist in, the respiration of the embryo-chick. The *albumen*, or *white* of the egg, is more fluid next to the shell-membrane, but becomes denser in its deeper parts, next to the yolk; it consists of 11·5 per cent. of albumen, 1 of fat, ·5 of saline matters, chiefly chloride of sodium, 2 of extractives, and about 84 per cent. of water. Within the white the large yolk is held in its place, or moored, by the two coils of elastic threads, named the *chalazæ*, *c c*, and, being lighter than the white, floats in it. Moreover, owing to the *chalazæ* being attached below the centre, or horizontal axis, of the yolk,

Fig. 119.

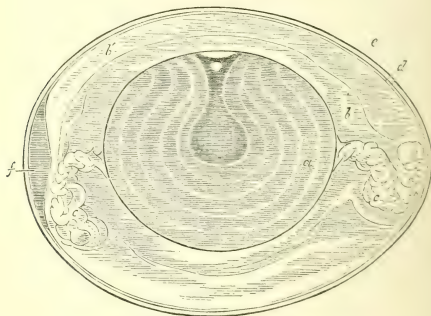


Fig. 119. Section of the hen's egg (Allen Thomson). *a*, microblastic yolk, enclosed by the vitelline membrane. *b*, inner dense part of albumen. *b'*, outer thinner or more fluid part. *c, c*, the chalazæ. *d*, double shell-membrane. *e*, the shell. *f*, the air-space between the two layers of the shell-membrane. The section of the yolk shows the halones, or concentric layers, also the central cavity or latebra, and the canal leading up from this to the cicatrix or disc at its summit.

particular portion of the surface of the latter, is always uppermost when the egg is laid upon its side; during incubation, therefore, it is next to the hen's body, and more accessible to air and light. The *yolk*, *a*, enclosed within its proper *vitelline*, or *vitellary membrane*, is of a pale-yellow colour, and of a lighter specific gravity than water; it is composed of 29 per cent. of fatty or oily matter, 17 of albumen, trace of phosphorised fatty matter, of cerebrie acid, and of salts, amounting in all to 2 per cent., and of 52 per cent. of water. It presents a fluid basis, composed of albumen in solution, mixed with the

granules; in this, are contained larger granules, and also larger bodies, called *yolk-vesicles*. These latter are *not true cells*, for they contain no nuclei; they vary from $\frac{1}{400}$ th to $\frac{1}{600}$ th of an inch in diameter, and are composed chiefly of fat particles aggregated together, but having no distinct cell-membrane or envelope around them, though they may be covered by an indistinct film of firmer albuminous substance. The outer parts of the yolk, as may be seen when it is boiled, are laminated or stratified, the several concentric layers being called *halones* or *haloes*, fig. 119; in its centre, is a cavity, known as the *central cavity* or *latebra*, fig. 119, in which the yolk is more fluid and contains *true nucleated cells*, mixed with free oil-globules of different sizes, floating in an albuminous fluid, and forming what is called the *white yolk*. This is an extension of the *germ-yolk*. Leading from this central cavity to that surface of the yolk which always floats uppermost, is a *channel* also filled with white yolk. At the upper end of this channel, is the pale, circular spot, or *disc*, known as the *cicatricula* or *germinal disc*, figs. 116, 117. This, which is the essential part of the germ-yolk, consists, even before the commencement of incubation, of two distinctly separable layers: the upper layer consists of firm and clear substance; the under layer, which is larger, is more opaque, and is composed of *nucleated cells*.

The Mammalian Ovaries and Ovum.

In the Mammalia, the organs in which the ova are formed, the so-called *ovaries*, are always double, one on each side. They are solid and not racemose, as in the Bird, and are of small proportionate size, corresponding with the smaller size of the *holoblastic* ova. They consist of a firm, indistinctly fibrous, vascular stroma, containing numerous vesicles, distended with a clear fluid, and named the *Graafian vesicles* or *follicles*, homologous with the *ovisacs* of Birds. These vary in size, from that of a pin's head to that of a pea, according to the stage of their maturity. The walls of each Graafian vesicle, consist of an enclosing vascular *stroma*, within which is a *membrana propria*, and, within that an *epithelial* layer or layers, forming the *membrana granulosa*. Embedded in a part of this latter, named the *proligerous disc*, is the minute holoblastic ovum, averaging about $\frac{1}{100}$ th of an inch in diameter. The size of the Human ovum, varies from $\frac{1}{240}$ th to $\frac{1}{120}$ th of an inch, that of the germinal vesicle, from $\frac{1}{760}$ th to $\frac{1}{2060}$ th of an

inch in diameter. In the Mammalian ovary, the ovisac, or wall of the Graafian vesicle, is not everywhere in close contact with the ovum, as in Birds.

At a certain period, a Graafian follicle bursts, not by a fissure, but by a small opening, and the ovum, with some of the nucleated cells of the *membrana granulosa*, a few of which have now acquired a club-shape and cling to the ovum in stellate masses, enters the funnel-shaped end of the so-called *Fallopian tube*, which corresponds with the oviduct in the Bird. Down this tube, the ovum descends by peristaltic action, perhaps aided by the movements of cilia, into the cavity of the *uterus* or womb, within which it undergoes its future development. Each ovary has its own Fallopian tube.

The emptied Graafian follicle, the walls of which have previously become thickened and vascular, is first filled with effused blood, which becomes absorbed. A yellow substance is then deposited in its coats, and, becoming plicated, forms the so-called *corpus luteum*; this is vascular, and consists of cells arranged in a columnar manner, mixed with soft fibres and a yellowish fat. It gradually disappears.

In the meantime, the lining-membrane of the uterus, with its columnar ciliated epithelium, has become thickened and more vascular, and certain glands within it are highly developed, so as to form perpendicular tubuli. The intertubular substance also undergoes hypertrophy, soon containing many new cells, with much fluid and fatty matter, thus forming a soft nutrient matrix, from which, by mere imbibition, the early ovum may be nourished. The *superficial stratum* of the altered mucous membrane, thus modified, becomes changed into the soft, pulpy, opaque membrane, known as the *decidua*, because it is thrown off with the embryo at birth. This membrane consists, after a time, of two layers, known as the *decidua vera*, and the *decidua reflexa*. The *decidua vera* is cribriform, being perforated by little orifices corresponding with the enlarged uterine glands; it lines the uterus, but is wanting at the orifice, and also at the openings of the two Fallopian tubes. It contains tortuous arteries proceeding from the uterus, together with large veins and venous sinuses, fine areolar tissue, nucleated cells, and soft granular matter. As this structure grows, it ultimately forms the *maternal portion* of the *placenta*, with its arteries, and venous *sinuses* or *lacunæ*, which is intended to convey nourishment to the future embryo, and to accomplish the respiratory changes in its blood. To son

part of the decidua vera, the ovum soon becomes adherent, whilst the *decidua reflexa*, as its name implies, covers in the ovum, either owing to a sinking-in of that little body, or to a rising-up of the decidual membrane. Ultimately the two portions of the decidua, coalesce, or the reflected part disappears. At the same time that the decidua generally, is becoming converted into the maternal portion of the placenta, the ovum itself, having been fertilised, grows rapidly, and undergoes remarkable changes in its interior—some relating to the formation of the embryo itself, others referring to the coats or membranes, which constitute its means of protection and of attachment to the maternal placenta. The outer vitelline membrane, which, from its thick and transparent albuminoid character, is named the *zona pellucida*, having lost the club-shaped adherent cells of the *membrana granulosa*, has developed around it, a thin but strong, whitish membrane, named the *chorion*, corresponding with the shell-membrane of the Bird's egg. The chorion is a fibrous membrane, having a layer of tessellated cells outside it. At first, smooth on its outer surface, it speedily becomes covered over with minute, soft, scattered knobs, which soon enlarge and form simple villi. These, composed of nucleated cells only, like the outer tessellated layer of the chorion itself, grow rapidly, and form swollen or club-shaped ends, which embed themselves in the soft structure of the early decidua vera, from which they doubtless actively absorb nourishment for the ovum. Afterwards, these primitive villi are replaced by other branched or tufted villi, which form the so-called *shaggy* or *villosus chorion*. These latter villi, after the others have disappeared, continue to enlarge, receive bloodvessels proceeding from the embryo now forming within the ovum, and so produce *vascular processes* or *tufts*, which project, or depend, into the venous sinuses or lacunæ of the maternal portion of the placenta. They constitute the *embryonal* or *fœtal portion* of the placenta, and, coming into close relation with the maternal blood, are the organs by which the nutrition and respiration of the embryo are henceforth carried on.

The chorion itself soon becomes lined with another membrane, named the *amnion*, which, as will afterwards be described, is derived from the embryo, and contains a fluid, the *liquor amnii*, which serves to protect the fœtus *in utero*, until the moment of its birth. The Mammalia are called *viviparous* animals.

The Ovaries and Ova of other Animals.

The description of the ovum of Mammalia and Birds, applies, in most respects, to the ova of the other Vertebrata; but there are certain peculiarities in some of these, and in the ovaries in which they are formed. The same parts in the Non-vertebrate animals, also require notice.

Reptilia.—In the Reptiles, which like Birds are oviparous, the ovary is also, as in them, racemose, and, as a rule, single. The yolk is large and covered with an abundant white, enclosed in a shell; but this is soft, instead of being firmly calcified. When the yolk is formed, the ova escape, by dehiscence, into the abdominal cavity, and are afterward received into the oviduct, which is placed at a considerable distance higher up. By these, as in Birds, they are discharged into the cloaca and thence are generally deposited externally, or oviparously. In the viper, the slow-worm, and green lizard, however, the development of the embryo takes place partially within the body of the parent; hence such reptiles are said to be *ovoviviparous*.

Amphibia.—In the Amphibia, the ovaries are double, and the ova are no longer, as in the Mammalia, Birds, and Reptiles, brought to maturity in *succession*, but *simultaneously*; being received into the oviducts, they are conveyed to the cloaca, and are then deposited in the water, either singly, in chains, or in masses. They are surrounded by a soft, mucous areolar tissue, which swells up in the water, keeps the ova apart, allows light and aerated water to get between them, and supplies temporary food to the young tadpoles.

Fishes.—In Fishes, the ovaries are also double and symmetrical, and are chiefly remarkable for the enormous number of ova developed in them. The number of ova in a codfish, has been found to be upward of 3,500,000, in a flounder 1,300,000, and in a mackerel more than 500,000. They are usually matured and deposited simultaneously, but in the case of migratory sea-fishes, like the herring, probably at successive periods. In certain Fishes which are *ovoviviparous*, the ova are few in number, and are deposited at short intervals. Most commonly, the ovaries have an excretory duct, continuous with them, like the *duct of a gland*, by means of which the ova are discharged into the water. The Cartilaginous, and a small number of Osseous Fishes, however, have no such excretory duct, but the ova pass into the peritoneal cavity, from which they escape, in the Cyclostomata, by an orifice on the under-side of the hinder part of that cavity, named the *abdominal pore*. In the sharks, a short tube, or rudimentary oviduct, first receives the ovum. In a sort of chamber, connected with this, the peculiarly-shaped, horny, protective case is secreted, like a chorion, in which the ovum is discharged.

In the Non-vertebrate animals, the ovaries are neither solid nor parenchymatous as in Mammalia, nor racemose as in Birds, Reptiles, Amphibia, and Fishes. In the higher forms, they consist of *sacs, caeca* or *tubuli*, which may be simple or ramified, and which, like a gland, have an attached or *connected* duct, named the *oviduct*, which, however, is not separate from the ovary, as in most Vertebrata. In the lower forms, the ova are developed, sometimes in a loose filamentous tissue, or in membranous plicæ, or upon stalks or processes in the interior of the

body, as in the Cœlenterata, or are actually embedded in its substance, as in the Protozoa.

Mollusca and *Molluscoida*.—In the Cephalopods, the ovaries are sacular. The ova are developed upon short processes in these sacs, and, when detached, leave a part behind, somewhat resembling a calyx. They are received into a special chamber, in which a protective covering is superadded to them. In the other Mollusca, the ovaries are found either arranged in strings, or in masses in the body-cavity. In the Lamelli-branchiata, the ovaries are follicular. In the Molluscoida, the ova, developed in follicles, are discharged by the oral cavity.

Annulosa and *Annuloida*.—In Insects, the eggs are generally numerous; the ovaries are cœcal, like the follicles of *glands*; they are double and symmetrical, but have a common outlet, in a sort of cloaca; frequently, the eggs are laid by aid of an *ovipositor*. The females of many Insects, have a reservoir, known as the spermatheca, like the bee. In the Crustacea, the ovaries are also double, each having its own outlet; they form cœca, usually branched, but in the lower forms, simple. The oviducts are often provided with a spermatheca. The Arachnida have elongated vesicular ovaries. In the Myriapoda, they are like those of Insects. In the Annelids, the ovaries have no oviducts, but the ova are set free in the perivisceral cavity. Amongst the Annuloida, in the vermiform Scolecida, the ovaries are either simple, or, more commonly, consist of much-ramified tubuli. The ova are numerous, and are discharged from a proper outlet, or from the anal orifice. In the Tænia, the ovaries are multiple, like the body; each segment has its ramified canals; in one species, the total number of eggs, in all the segments, is said to be 64,000,000. In the Rotifera, the ovary is single and sacular; the young are sometimes developed, more or less completely, within the parent animal. In the Echinodermata, the ovaries are ramified tubes, modified according to the shape of the body of the animal, there being usually a pair in each arm or segment: but in the Holothurida, they are single, have terminal clusters of cœca, and open near the mouth.

Cœlenterata.—In some of these, as in the Physograde and Cirrhirgrade forms, the ova are developed in clusters on the base of the cirrhi. In the Pulmograde forms, they are developed in sacs in the body-cavity. In the Actinozoa, they adhere to plicated folds of membrane, in that cavity. There are no oviducts, and the ova are discharged from the oral aperture.

Protozoa.—In these animals, the germ-cells, scarcely appear like true ova; they form on, or in, the substance of the parent.

From the preceding account, it is evident that the ovaries are homologous with glands; so that the germ-cells, or ova, may, as well as the sperm-cells, be regarded as the products of a special nutrient secretive act.

The Fertilisation of the Ovum.

The fertilisation of the ovum, whether it occur within, or without, the body of the ovigerous parent, requires the contact of the male fertilising agent, which, in many cases, has

been recognised under the microscope, by the actual presence of *spermatozoa* upon, or even within, the zona pellucida of the Mammalian ova, or upon, or within, the vitelline membrane in other ova.

In the Mammalia, fertilisation occurs in the Fallopian tube, or in the uterus. In Birds and Reptiles, and in the higher Cartilaginous and a few Osseous Fishes, which are ovoviviparous, it takes place as the yolk enters the oviduct, before it receives its coating of albumen. In Amphibia, it happens at the time of deposit of the ova, and in Fishes, with the exception of a few, immediately after. In the Mollusca and Molluscoida, Annulosa and Annuloida, and Cœlenterata, fertilisation occurs within the body, whether the sexes be distinct, or whether

Fig. 120.

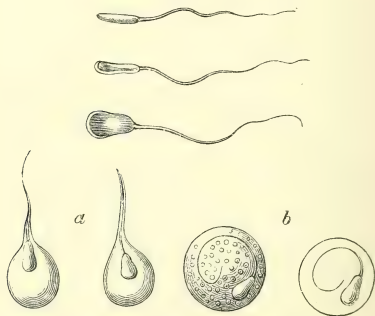


Fig. 120. *a*, spermatozoa of the squirrel. *b*, spermatozoa of the dog, still enclosed in the sperm-cells. Three spermatozoa are shown free, above. Very highly magnified (Wagner, Leuckhardt).

hermaphrodite individuals contain both ovaries and fertilising organs. Even in the Protozoa, separate nuclear bodies exist, which combine or conjugate, previously to the reproduction of new individuals.

In the Mammalian ovum, it is said that the germinal vesicle approaches one side of the germ-cell, and even has its germinal spot turned in the same direction—that is, towards the side directed to the place of rupture in the Graafian follicle. Such a movement would certainly facilitate the access of the fertilising agent to the germinal vesicle and spot, that is, to the nucleus and nucleolus of this primitive cell.

In the Frog's spawn, the spermatozoa have been seen in the jelly-like envelopes of the ova, and also within the ovum. In certain Osseous Fishes, a minute, funnel-shaped aperture, named the *micropyle*, forms, at one period, in the vitelline membrane, and admits the entrance of the spermatozoa. A micropyle has also been seen in the ova of the Lamellibranchiate Mollusca, of certain Insects, and of some Echinodermata. In these cases, the vitelline membrane is relatively thick. No micropyle has been seen in any of the Vertebrata, excepting in Osseous Fishes.

DEVELOPMENT.

CHANGES IN THE OVUM. FIRST FORMATION OF THE EMBRYO, AND ITS APPENDAGES.

The first essential change which occurs in the fertilised ovum, is the so-called *cleavage* or *segmentation* of the yolk. In the *holoblastic* Mammalian ovum, the yolk is seen to be agitated by a peculiar movement—to elongate, contract itself in the middle, and then to divide into two. Each half rapidly undergoes further movement, contraction, and division, so that it now consists of four parts. By subsequent subdivision, these next form eight, sixteen, thirty-two parts, and so forth. The first effect of this cleavage, is to transform the yolk into a mulberry-looking mass; but, after repeated subdivision, the surface again becomes smooth, and uniform or granular, and is composed entirely of an immense number of polyhedral nucleated cells, which form a layer within the vitelline membrane, and constitute the so-called *germ-sac* of Coste, or *blastodermic vesicle* of Bischoff. The central fluid part becomes clear. The segmentation of the entire yolk, has been observed in all cases of development from *holoblastic* ova, even in Non-vertebrate animals. In the eggs of certain Branchiostomopods, a remarkable *revolution* of the yolk takes place, subsequently to the period of its segmentation, the yolk turning first in one way and then in another, within the vitelline membrane; this is said to depend on ciliary movements. In the *meroblastic* ova of the Cephalopods, certain Fishes, Reptiles, and Birds, only a part of the yolk, viz. the *germ-yolk*, in the neighbourhood of the germinal vesicle, undergoes this

segmentation, the result being the formation of the *germina disc* or *cicatricula*, already mentioned, from which, however

Fig. 121.

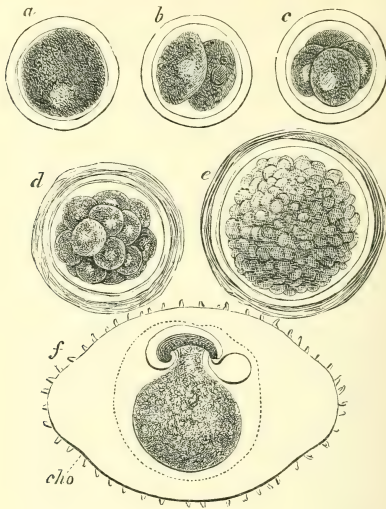


Fig. 121. Changes in the ovum of a Mammalian animal, after fertilisation (Allen Thomson). *a* to *e*, successive stages in the segmentation or cleavage of the yolk. *a*, yolk still undivided; *b*, cleft into two masses, each surrounding a nucleus; *c*, divided into four; *d*, non-divided; *e*, mulberry-like stage of subdivision, to form the blastoderm. The small nucleated yolk-masses have no distinct envelopes. The ovum has acquired a thicker coat, or chorion. After this, the surface of the yolk again becomes smooth, and composed of nucleated cells, having true envelopes. The diagram *f* shows the relations of the embryo and its so-called appendages. The dark curved body is the *embryo*; beneath it, is the open part, leading by the *vitelline duct*, to the *yolk-sac*, or future *umbilical vesicle*. Immediately surrounding the embryo, above it, and at each end, is the sac of the amnion, or true *amnion*; the dotted line shows the false amnion. Outside this, is the *chorion*, *cho*, with its rudimentary *villi*. The bladder-like organ, projecting from the hinder end of the embryo, is the *allantois*.

an extension of a single layer of cells, proceeds over the unsegmented portion of the yolk, forming the so-called *germinal sac*.

This yolk-cleavage is a phenomenon of *cell-division*. It is stated by Müller, Gegenbauer, and Leydig, that the germinal vesicle, or nucleus of the cell of the ovum, and the germinal spot, or nucleolus of that cell, are directly concerned in this process. The nucleolus and nucleus are said to divide successively into two, four, and many nuclei; around which, the yolk, apparently governed by these successive subdivisions of the nucleus, gathers for the development of the nucleated cells. In the last generation, these cells acquire distinct cell-walls. According to others, in certain animals, the germinal vesicle and germinal spot, the primitive nucleus and nucleolus, disappear completely, immediately after fertilisation occurs, and their future destiny cannot be traced; but a *fresh cell* or *nucleus* is supposed to be formed, around which the yolk gathers, and by the repeated subdivision of this, into two, four, eight, and so forth, the cleavage of the yolk is accomplished. The first cell from which these arise, has been named the *embryo cell*. According to the former view, the cells which appear on the surface of the yolk, and out of a part of which, as we shall immediately see, the embryo itself begins to be evolved, are derived *directly* from a nucleus, once forming a part of the maternal organism. According to the latter view, they, and therefore the embryo, are developed *indirectly*, or independently, after the solution and diffusion of the *primitive* germinal vesicle and spot, with the fertilising agent, in the substance of the yolk. In the flowering plants, also, the nucleus or germ-vesicle of the ovule, or ovum-cell, is said, by some, not to participate in the formation of the cells from which the embryo plant is developed. Whichever of the preceding views be adopted, the cleavage of the yolk is attributed, however, to the formative force, known as the *germ-force*, resident in the first-formed nucleus and nucleolus, and continued in all their successive subdivisions. The germinal vesicle and spot, as already stated, are said to disappear even in unfertilised Bird's ova.

The formation of the layer of nucleated cells which constitute the *germ-sac* of the holoblastic, or the *germinal disc* of the meroblastic, ovum, as a result of the cleavage of the yolk, is altogether preliminary to the formation of the embryo, which cannot yet be recognised. In the Non-vertebrate *holoblastic* ovum, as, for example, in the Nematoid *Ascarides*, these cells soon aggregate into a more or less coiled opaque mass, which assumes the shape of the embryo, and then, by further develop-

ment, actually forms the young animal. This is also the case in the Echinodermata, the smaller Crustacea, and Arachnida, the Insecta, and the Mollusca, except the Cephalopods. But in the higher animals, with holoblastic ova, such as the Cyclostomatous Fishes, the Amphibia, and the Mammalia, the cleavage-cells form, at a certain part of the germ-sac, a small opaque hemispherical mass, which soon spreads out into a *disc-like* layer, and constitutes the so-called *germinal disc* or *area*, *area germinativa*, *embryo-spot*, or *blastoderm*. It is the central part of this, which is directly concerned in the formation of the embryo. In the Molluscous, and other animals just enumerated, no such germinal area is found. In all the *meroblastic* ova, whether of Non-vertebrate or Vertebrate type, as is well seen in the hen's egg, the *cicatricula*, or *germinal disc*, already described, constitutes this germinal area or embryo-spot.

In this area, as in that of the higher holoblastic ova, the first traces of the embryo are formed. Amongst the Non-vertebrate types, those of the higher Arachnida, and Crustacea, appear as a certain number of *opaque spots*, having a beautiful symmetrical arrangement, whilst in the Cephalopods, they commence by a small number of primitive masses. In the Vertebrate holoblastic or meroblastic ova, the commencement of the embryo is always indicated, amongst other things, by the appearance of a *linear primitive streak*. This is quite characteristic of the Vertebrate type of ovum, not occurring even in the elongated Annulose type. The evolution of the Vertebrate embryo, can alone occupy our attention here. That of the chick *in ovo*, will be generally followed; but the peculiarities of the ovum of the Mammalia, will also be indicated.

When first formed, the appearance of the *blastoderm*, or blastodermic layer of the germinal area, is nearly or quite uniform, all its nucleated cells being alike, and the result of a homogeneous evolution. But soon, a heterogeneous development ensues, cells of different character, and collected in peculiar situations, appear, and, by more special aggregations, and wider differentiations, the various parts which form the embryo, its organs, tissues, and appendages, are evolved.

First, the germinal area or disc increases in size or thickness, by the formation of new cells; as already mentioned, it very early consists of two layers, named the *upper, external*, or *serous*, and the *lower, internal*, or *mucous germinal lamina*, or *plate*; between these, a *middle* germinal layer, lamina, or plate, is soon formed, but rather in connection with the serous

ayer. The internal layer, epithelial in structure, is soon prolonged over the germinal sac, which covers the yolk; the outer layer also extends itself, but the middle layer does not pass beyond the limits of the embryo-spot. As the germinal area enlarges, it presents a central transparent region, known as the *transparent area*, or *area pellucida*, around which is a denser portion, named the *opaque area*, or *area opaca*; beyond this, is the *vitelline area*. The transparent area is at first circular, but soon oval, and afterwards pear-shaped; in it, the first rudiments of the embryo appear, in the form of a linear oblong mark, or *streak*, called the *primitive trace*, or *groove*. This consists of a median or *axial* furrow, bounded by two lateral longitudinal plates, named the *laminae dorsales*, which enlarge and elongate, as the area itself becomes larger and pyriform in outline. Beneath this groove, immediately below its floor, appears a delicate, semi-opaque thread, at first cellular, but soon becoming cartilaginous, named the *chorda dorsalis* or *notochord*, which part, so characteristic of the Vertebrate type, is recognisable in the chick, as early as 18 hours after incubation. These are the rudimentary parts of the embryo, one end giving origin to the head, and the other corresponding with the tail. The position of these rudiments is remarkably constant in the hen's egg, always lying transversely to the long axis of the egg; as the embryo-chick develops, it turns upon its side, so that the forepart of the head usually faces the narrow end of the egg.

In the rudimentary stage just described, a vertical section cross the embryonal line of the germinal area, would show the edges of the three *germinal layers of the blastoderm*, with the primitive groove or furrow in the centre, and the cross-section of the *chorda dorsalis* beneath it.

From these three layers, the parts of the future embryo are thus evolved. From the upper external or *serous* layer, also named the *sensorial* layer, are developed, along its axial portion, the cerebro-spinal nervous axis, and the organs of the senses; and, from its lateral portions, the cuticle or outer skin, with its epidermic appendages, the feathers, bill, and claws, and in mammalia, the nails and hairs; lastly, the sebaceous and sudoriferous cutaneous glands and the Meibomian, ceruminous, and mammary glands. From the *middle* layer, also called the *otario-sexual* layer, are developed, by complicated metamorphoses of its substance, the bones, the muscular system, the peripheral spinal nerves, the sympathetic nerves, the heart, bloodvessels, and lymphatic system, the so-called ductless

glands, and the reproductive organs; also, next to the external layer, the true skin, and, next to the internal layer, the muscular and submucous coats of the alimentary canal. Lastly, from the *internal* layer, also called the *mucous* or *intestinal* layer, are developed, the epithelial lining of the alimentary canal, and all its glandular extensions, such as the mucous, gastric, and intestinal glands, the pancreas and the liver, also the lungs and respiratory passages, and the urinary apparatus, including the bladder, ureters, and kidneys.

Whilst, therefore, the middle layer gives rise, by very striking differentiations, to a great variety of tissues, the upper and lower layers, except that part of the former which gives origin to the brain and spinal cord, produce textures composed of simpler forms of cell-tissue.

These layers also contribute, in a manner to be presently described, to the formation of three parts or *appendages* external to the body of the embryo—viz., the *amnion*, the *yolk-sac* or *umbilical vesicle*, and the *allantois*.

GENERAL DEVELOPMENT OF THE EMBRYO AND ITS APPENDAGES.

The borders of the primitive or vertebral groove, including parts of the external and middle layer (the former named the *medullary plate*, and the latter the *vertebral plate*), rise up on each side, and ultimately unite along the middle line, to form a *canal*, containing the rudiments of the future brain and spinal cord; the anterior part or cephalic end of this canal, becomes more expanded than the rest, whilst the posterior part tapers to a point. In this way, the so-called *neural cavity* (vol. i. p. 134) of the future animal, is formed *above* the *chorda dorsalis*, traces of which are, for a time, found passing through the bodies of the growing vertebræ. Soon, from the vertebral plates, where these turn upwards, the external and middle layers extend sideways, constituting the so-called *lateral plates* which, growing downwards, and bending inwards, form the walls of the abdomen, and enclose a cavity which is placed *beneath* the *chorda dorsalis*, immediately in contact with the yolk; this ultimately constitutes the *hæmal* or *thoracico-abdominal* cavity of the future animal; it soon contains the heart and great bloodvessels, and the rudiments of the alimentary canal, which is completed by a corresponding folding-in of the internal blastodermic layer which lies immediately upon the yolk.

The embryo, by the bending in of its sides, next appears to be raised from the yolk, and partially shut off from it, by a part of constriction which takes place, first beneath the head and the caudal extremity, and afterwards at each side. Ultimately, this constriction shuts off the body of the embryo from the yolk-sac, which then communicates only by a narrow passage, the *ductus vitelli*, or *vitelline duct*, with the central space in the interior of the embryo, now the rudimentary alimentary canal, lying in the hæmal cavity. The yolk-sac thus cut off, shrinks, and forms the *umbilical vesicle*. The head of the embryo, now free, bends down towards the yolk, and forms the *cephalic flexure*. At the same time, a delicate transparent membranous fold, derived from the external germinal layer of the blastoderm, rises, like a hood, over that part of the embryo; a similar, but smaller, fold rises over the free caudal extremity, and, on each side, where the lateral plates bend in to form the constriction just described, corresponding folds arise. These folds are double; they grow, and at length meet over the back of the embryo, and coalesce so as to form, in their innermost layer, a complete, but delicate, closed sac, called the *amnion*, which, in the chick, is perfected as early as the third day of incubation. This is at first close to the embryo, but it soon expands, and carries with it the outer layer of the same folds, which afterwards reaches the shell membrane in the Bird, but in the Mammalian ovum, becomes attached to the inner surface of the chorion, and so forms the *false amnion*. The sac of the amnion surrounds the vitelline duct, in a sort of sheath, and thence becomes continuous with the skin covering the body of the embryo (see fig. 121).

The amnion is, thin, transparent, and non-vascular. It consists, at first, of a structureless basement membrane, lined with a delicate squamous epithelium; afterwards it contains uniform cells, and a fine areolar tissue, and, in Birds, even non-striated muscular fibres. Its fluid contents, the *liquor amnii*, usually alkaline, consist of water, having in solution from 1 to 3 per cent. of solid matter: this is composed of a little albumen, traces of urea and uric acid, allantoin and other extractions, salts, such as lactate of soda and sulphate and phosphate of lime, and lastly, sebaceous matter, epidermoid scales, and minute hairs thrown off from the embryo.

The amnion, considered as an appendage of the embryo, is chiefly protective, but may be respiratory or emunctory. It is present not only around the embryo of the Bird, but also

around that of Mammalia and Reptiles. The embryos of the Amphibia and the Fish, however, which are developed in, and surrounded by, water, are destitute of an amnion, no such covering being formed, and no folding over of the external blastodermic layer taking place, as in the ovum of the Reptile, Bird, and Mammal.

The *umbilical vesicle* or *yolk-sac* already mentioned, may also be regarded as another appendage of the embryo. It is formed, as just described, by the lower part of the yolk-sac, surrounded by an extension of the innermost germinal layer, and connected with the intestinal canal of the embryo, by the constricted passage named the *vitelline duct* (fig. 121). It is not only external to the body of the embryo, but also outside the cavity of the amnion. Very early, certain bloodvessels are developed in the middle germinal layer of the embryo, and, spreading into a network of vessels, they extend upon the surface of the yolk, and form the so-called *vascular area*. Two special branches, named the *omphalo-mesenteric arteries*, convey blood from the embryo through this area, and a vascular membrane is thus formed, which gradually covers the umbilical vesicle, yolk-sac, and also extends itself, at least in the Birds' and Reptiles' eggs, by numerous projecting folds, into the substance of the yolk. From the substance of the yolk, these bloodvessels absorb dissolved nutrient material; and, for a time, the blood contained in them, is aerated by interchanges of carbonic acid and oxygen between it and the other fluids of the egg or ovum. In the Bird, the yolk-sac is very large; it is gradually drawn into the abdomen of the chick, and may be found in that cavity after the chick is hatched. In time, its contents are gradually absorbed, and its remains are frequently traceable as a slight blind sac or stem, the *vitelline cæcum*, connected with some part of the small intestine. Similar changes are observed in Reptiles. In the Plagiostomatous Fishes, as in the sharks, the yolk-sac remains, for a long time, suspended to the abdomen of the young fish. In the Osseous Fishes, the yolk, being small, sooner disappears. In the Cyclostomatous Fishes, and in the Amphibia which have holoblastic ova, the yolk-sac is still smaller and more transitory. Lastly, in the Mammalia, it is very minute, but undergoes slight growth, especially in the Carnivora and Rodentia. It is found, after a time, as a circular, pale-yellow disc, attached to the amnion, and having no further function; sometimes, as in Ruminantia, it is completely absorbed.

Besides the amnion and the yolk-sac, another most important appendage of the embryo in Birds, Reptiles, and Mammalia, remains to be described. This is the so-called *allantois*. In the Bird's egg, it appears as a small eminence, at first consisting of nucleated cells, but soon becoming vascular, situated on the under-side of the embryo, close to its caudal end. It is derived from portions of the internal and middle germinal layers, which, in this situation, form the intestinal part of the alimentary canal. The allantois soon becomes a hollow protrusion of the intestinal wall, growing out, in the form of a sac or bladder, beyond the body of the embryo, and being placed, like the umbilical vesicle, *outside* the sac of the amnion (fig. 121). It carries out with it, numerous bloodvessels, which are developed in the middle germinal layer, and are connected with the great vascular trunks of the hinder part of the embryo. It quickly extends itself, till it reaches the inner surface of the shell-membrane of the egg, over the interior of which it spreads, with its walls closely applied to each other, so as to form a double membrane, the outer layer of which, in contact with the shell-membrane, retains its bloodvessels, whilst those of the inner layer, next to the white of the egg, become shrunken. The hollow stalk or stem of the allantois, which is situated within the embryo, opens into a small cavity, developed in connection with the lower end of the intestine, named the *progenital sinus*, which forms the rudimentary *urinary bladder*. Between this cavity and the opening in the walls of the embryo, through which the vitelline duct passes to the umbilical sac, hence called the *umbilical opening*, the allantoid canal closes, and is converted into the *urachus*, or *superior ligament of the bladder*. Outside the umbilical opening, the bloodvessels of the allantois, now named the *umbilical vessels*, ramify in the outer layer of the allantois, next to the shell-membrane, forming a densely vascular structure applied to the inner surface of the whole shell, separated from it only by the shell-membrane. In an early stage of development, the allantois of the Bird, is contractile, and acts as a sort of urinary bladder, its fluid containing urea, allantoin, sugar, certain salts corresponding with those of the blood, with slight traces of albumen. It receives, indeed, the secretions of certain organs known as the *Wolffian bodies*, or *primordial kidneys*, and also those of the rudimentary kidneys themselves. Its superficial vascular layer next to the shell-membrane, which has been named the *endochorion*, is the active respiratory

organ of the embryo bird, after the vessels upon the yolk-sac have ceased to be sufficient for this purpose. The blood to be aerated, passes from the embryo through the umbilical arteries on to the allantois, and returns to the embryo by the umbilical vein. As the period of hatching approaches, the vessels of the allantois and this membrane itself, become partially dried; the young bird chips the egg, and begins to breathe by its lungs. By the time it escapes from the shell the allantois and its vessels are quite desiccated.

The allantois is present also in Reptiles, the shell of the egg of which is soft and thin, and the oxygenation of the blood easily performed. In Amphibia and Fishes, there is no allantois, the respiration of their embryos, which are entirely aquatic, being at once accomplished by means of gills, so that no allantois is needed.

In the Mammalia, however, the allantois is invariably present, and fulfils a most important office; for it is the means of conveying outwards, from the embryo to the maternal structures, the vessels which connect the two, and serve in the functions of nutrition and respiration. Its inner part forms, as usual, the urachus, and joins the apex of the future urinary bladder; and its outer part, for a time, constitutes the so-called *allantoid sac*. This outer part extends itself, till it reaches the inner surface of the chorion. As already described, this last named structure is formed upon the altered vitelline membrane and soon becomes covered, on its outer surface, with little knobs; these are developed into temporary villous processes composed entirely of nucleated cells, and employed in absorbing nourishment for the early mammalian embryo. After a time these simple villi disappear, being, as it were, obliterated by the growth and distension of the chorion. But then, the chorion itself, and the *outer layer* of the amnion, or *false amnion*, which is now in close relation with the chorion, becomes the seat of development of other processes, which, with a thin covering of cells from the chorion itself, form the ramified tufted villi of the so-called *shaggy chorion*. As the allantoid sac of the Mammalia, with its contained bloodvessels, grows it reaches the inner surface of the chorion, and, its vessels entering the villous processes of the latter, form loops in the interior. These processes, now vascular, and constituting the *embryonal* or *fœtal portion* of the placenta, penetrate, through the decidua, into the *maternal portion* of the *placenta*, projecting into its venous sinuses and lacunæ, and form the so-

alled *foetal villi*. These are covered by their own epithelium and basement membrane, and also by a loose layer belonging to the lining-membrane of the maternal venous sinuses. The blood of the Mammalian embryo, passing along the umbilical arteries, upon the allantois, circulates through these foetal villi, which are themselves bathed with the maternal blood. The two bloods come into close relation, being separated only by the most delicate tissues, but they do not intermingle. In this way, nutriment is absorbed from the maternal blood, for the maintenance of the growth of the embryo; and possibly effete matters are especially eliminated from the embryonal blood. This latter blood is oxygenated by a respiratory process, consisting of an interchange of carbonic acid and oxygen between the embryonal and maternal blood, just as occurs in the gills of the Amphibian tadpole, and of the fish, which are bathed in water. The blood in the umbilical arteries of the embryo, is, as we shall see, nearly all dark or venous blood; that in the maternal venous sinuses, is really arterial, for the maternal portion of the placenta contains no capillaries, the branches of the uterine arteries which enter it, terminating at once in the venous lacunæ, from which the true uterine veins pass obliquely. Having been properly purified and nourished, the embryonal blood returns from the placenta, enters the umbilical veins, and through them, reaches the embryo again. In the Reptile and Bird, the respiration of the embryo takes place between the embryonal blood in the vessels of the allantois, and the atmospheric air in the fluids of the egg, or outside the shell-membrane: in neither class, do the vessels of the allantois or the branches of the umbilical vessels, penetrate the outer coverings of the ovum, as occurs in the Mammalia generally.

The exact relations of the allantoïd sac and its vessels, with the chorion, and especially the extent to which it covers the interior of that coat, vary in the different Orders of Mammalia. In the Monotremata and Marsupialia, for example, the allantois is small and pear-shaped; its vessels are merely arborescent, and do not penetrate the chorion. Hence there is no special organ, or *placenta*, intermediate between the embryo and the uterine walls, and these animals are therefore named *Implacental Mammalia*.

In the porpoise, the pig, the horse, and, it is said, in the camel tribe also, every part of the chorion and the allantoïd endochorion, which are coextensive, is covered with vascular

processes; these enter the hypertrophied uterine membrane at all points, and form the so-called *diffused placenta*. In the Ruminants, with the possible exception of the camels, the vascular endochorion, or developed allantois, is also coextensive with the chorion; the vascular processes project, and attaching themselves to the uterus at certain definite scattered points of the surface, form the *embryonal cotyledons*; these consist of clusters of *ramified* villi, which fit into corresponding ramified canals, arranged in cup-shaped depressions of the uterus, called the *maternal cotyledons*. No decidua exists, in these cases, between the embryonal and the maternal tissues, and they are easily detached from each other. The blood in both, is brought into close proximity, but the vessels of each are independent, and the two bloods do not intermingle. In the dog, cat, and Carnivora generally, the ovum, at first round, afterwards becomes oval, fusiform, or elongated, and occupies a compartment in the elongated uterus. The endochorion, or allantoic sac, is very extensive; but the villous processes, absent from the ends of the ovum, form a broad zone around its middle. A true decidua exists, and the combined structures constitute the *zonular placenta*. In the Rodentia, as is well seen in the rabbit, the allantoic sac reaches a small part only of the inner surface of the chorion; at this point alone, permanent vascular processes are developed, which, entering the hypertrophied uterine membrane, part of which forms a decidua, constitute a *discoid placenta*.

In the formation of the *discoid human* placenta, it is noticed that the allantois is very small, appears early, and soon wastes; it reaches the chorion at only one point, not spreading out coextensively with it; and it conveys outwards, as usual the umbilical arteries, the branches of which enter the permanent villous processes of the shaggy chorion, or foetal villi; these are limited to one part of the ovum, penetrate the decidual and hypertrophied portion of the uterine walls, and enter the maternal venous sinuses.

The *two* umbilical arteries and *one* umbilical vein, are supported upon the remains of the now impervious allantois, which grows into a soft mucous connective tissue; with these parts also are found the wasted vestiges of the vitelline duct, with its atrophied omphalo-mesenteric artery and veins; these structures becoming elongated, and surrounded with a tubular process of the amnion, form the umbilical cord or navel-string. This cord is, therefore, connected with the placenta at one end,

ad with the navel of the embryo at the other. Its vessels are always more or less spirally twisted.

At the birth of the Mammalian embryo—an event which, with the human infant, happens at the end of the fortieth week—the foetus and its membranes are detached from the inner surface of the uterus. The embryonal vascular portion of these membranes, whether it be a diffused, cotyledonous, zonular, or discoid placenta, is always detached. In the case of the zonular and discoid forms of placenta, where a true decidua is developed, a part of the maternal tissues is also separated at the same time. Where there is no decidua, as in the diffuse and cotyledonous forms, the foetal villi are merely detached from the surfaces or recesses into which they fit. In the latter cases, parts of the maternal tissues, especially of the veins and venous lacunæ, come away. Hemorrhage is ordinarily quickly arrested, owing to the obliquity of the passages leading into the deeper uterine veins, and to the firm contraction of the uterine walls. If these become relaxed, arterial, but not venous, hemorrhage may occur.

DEVELOPMENT OF THE ORGANS.

The share taken by each of the three germinal layers of the blastoderm, in the formation of the several systems of organs, having been described, their special development may now be considered.

The Skeleton, Muscles, and Integuments of the Body.

The *vertebral column* is developed from the vertebral plates of the middle germinal layer, found on each side of the vertebral groove and chorda dorsalis. As the vertebral groove passes along the back of the embryo, first opposite the cervical and dorsal regions, small square masses are seen on each side of the median line, in the inner thicker portion of the vertebral plates. These were formerly considered to be the rudiments of the bodies of the vertebræ only, and were named the *primitive* or *primordial vertebræ*; but they are better named the *dorsal segments*, for other structures, besides the vertebræ, are developed from them. In the thoracic region, the posterior ends of the ribs, and, throughout the whole length of the vertebral column, the roots of the spinal nerves, together with the ganglia on the posterior roots, which are of great proportional size, the spinal muscles, and the cutis covering these parts,

are thus formed ; a small portion only, therefore, is developed into the future vertebræ. The part which forms the skin and spinal muscles, is named the *dorsal plate* or division, whilst the rest is called the *ventral plate* or division. The innermost portion of this latter, which is called the *vertebral plate*, grows inwards, and surrounds the chorda dorsalis, so as to enclose it in a thick, continuous, membranous sheath ; this divides anew, transversely, into annular portions, corresponding with the bodies of the future cervical, dorsal, lumbar, sacral, and coccygeal vertebræ, into which they are developed, by passing first into a cartilaginous, and then into an osseous, state. The body of the atlas joins the axis, to form its odontoid process. The remains of the chorda dorsalis are traceable, for a long time, through the centre of the bodies of the vertebræ, but ultimately they become absorbed. In the lowest or Myxinoid Fishes, however, the chorda dorsalis is recognisable throughout life. Between the vertebræ thus formed, an intermediate soft tissue becomes developed into the *intervertebral substances*, in which the notochord persists, as the softer fibrocartilaginous centre. Whilst the bodies of the vertebræ are thus produced, another portion of the dorsal division of the vertebral plates, ascends towards the back of the embryo, grows around the vertebral groove, and then forms the *arches* and *spinous processes* of the vertebræ, so completing the vertebral column. These cartilaginous arches first close in the dorsal part of the column, and then meet everywhere, except opposite the coccyx, and sometimes at the lower end of the sacrum ; the non-formation or non-union of these arches, constitutes *spina bifida*.

At the anterior or *cephalic* end of the embryo, as already mentioned, the sides of the vertebral groove, composed of the medullary and vertebral plates of the external and middle germinal layers, expand, and, meeting above in the middle line, enclose a space which forms the rudiment of the cranium and its contents. This is soon marked off into *three pairs* of symmetrical sacs or dilatations, named the *cerebral vesicles*, which, bending down towards the yolk, form the *cephalic flexure*, or bend of the neck. In that part of the walls of these vesicles, which corresponds with the middle germinal layer, the *cephalic capsule* or *primordial skull* is formed ; this is at first membranous, then partly cartilaginous, and ultimately bony. Into the floor of this cavity, the anterior extremity of the cartilaginous notochord, or chorda dorsalis, penetrates

only a short distance, reaching, in the middle line, as far forwards as the future *sella turcica* in the sphenoid bone, which lodges the pituitary body. The base only of the primordial skull, becomes cartilaginous, like the bodies of the primitive vertebræ; the sides and upper part of the cephalic capsule remain membranous. The primordial skull does not divide into transverse segments, like the rudimentary annular vertebræ. Its cartilaginous portion is developed into the base and sides of the occipital bones or basi- and ex-occipitals, the *alæ majores* of the sphenoid or ali-sphenoids, and the pre-sphenoids and orbito-sphenoids or *alæ minores*, also into the *turbinate* bones, the *median portion of the ethmoid* bone, and the cartilaginous *nasal septum*. The *vomer*, however, is formed from a membrane, below the septum. The upper part of the *occipital* bone or supra-occipitals, the *parietal* bones, the *squamous* part of the *temporal* bones, the *frontal* bones, and the *nasal* bones, are developed as distinct *opercular* bones, directly from special centres of ossification in membrane, and not from cartilage. The *petrous* and *mastoid* parts of the temporal bone, and the floor of the tympanum, are developed from osseous centres in the basal cartilage; the *tympanic ring* arises from a fibro-cartilage, specially connected with the ear. The bones of the *face*, including the *upper* and *lower jaws*, also the *ossicles of the ear*, the *styloid* process of the temporal bone, and likewise the *hyoid* bony apparatus, are developed from the so-called *visceral* or *branchial arches*, which are formed, as will be hereafter described, from the lateral ventral plates of the cephalic portion of the embryo.

Opposite the trunk or body of the embryo, the outer or lateral part of the ventral plates, extends downwards from the vertebral plates, to surround the hæmal cavity or future *thoracic-abdominal* chamber of the embryo. Within these plates, in the thoracic region, opaque lines appear, which ultimately form the *ribs*; where they close below in the middle line, the rudiments of the separate pieces of the *sternum* are developed; these may remain ununited in the middle line, constituting a rare and remarkable deformity—*fissura sterni*. In a similar manner, the *pelvic* or innominate bones, the *ilium*, *ischium*, and *pubes*, are formed near the hinder part of the body; and the *scapular* arch, consisting of the *scapula* and *clavicle*, at the fore-part of the trunk.

A little later, the rudiments of the *limbs* appear, like small knobs, on each side of the trunk. In the centre of these, which

consist of extensions of the middle germinal layer, the rudiments of the bones are soon seen, and ultimately become distinguishable as the bones of the arm, forearm, and hand, or of the thigh, leg, and foot. As the dorsal segments give origin, not only to the vertebræ, but also to the neighbouring muscles and to the covering of the cutis, so the lateral plates, which produce the ribs and sternum, and the scapular and pelvic arches, and also the extensions of those plates which form the future limbs, not only give origin to the bones of those parts, but also to the corresponding muscles and cutis. The epidermis or cuticle covering all these parts, and, indeed, that of the whole body, is formed upon them, by the common *external germinal layer*.

At first, the future skeletal parts are soft, and composed of cells but slightly differentiated from the rest of the cells of the germinal layer or blastoderm; by degrees, these parts become cartilaginous or membranous, and ultimately they undergo ossification. The process of ossification, with its order and times of occurrence, will be hereafter noticed.

Not only are all the muscles, and also the true skin thus developed, as well as the bones, ligaments, and joints, but likewise their respective vessels and lymphatics, and the nerves, both motor and sensory, which constitute the peripheral part of the spinal and cranial nerves, excepting those of special sense. The first muscles to be developed are those of the vertebral grooves, next the muscles of the neck, then those of the abdomen, afterwards those of the limbs, and lastly the facial muscles. The limbs are at first like simple buds, derived from the lateral plates; but they soon show divisions into their respective segments, and expand and flatten at their extremities; these next exhibit indentations corresponding with the future toes or fingers, which, for a time, are webbed. The upper limb is usually developed before, and more quickly than, the lower one. The limbs are at first simple masses of blastema, which gradually change into cartilage, bone, muscle and skin. On the surface of the body and limbs, a layer of polygonal epidermic cells is very early traceable; this is the commencement of the cuticle. The papillæ of the skin, the rudiments of the hairs, feathers, nails or claws, and also of the cutaneous glands, afterwards appear.

The *mammary glands*, when first formed, resemble the cutaneous glands, consisting of solid processes derived from the epidermic layer, and penetrating the cutis; these afterwards

branch out, and ultimately become hollowed, to form the mammary ducts and vesicles.

The Brain and Spinal Cord.

The sides of the vertebral groove are lined on their surface, by a special layer of blastema, known as the *medullary plates*, derived from the *external* germinal layer. When the groove and its cephalic expansion are closed, first in the neck, and then along the middle line of the back of the embryo, a *medullary canal* with a cephalic enlargement, is formed; and the medullary plates, becoming thicker and growing from below upwards, are converted, subsequently to the appearance of cartilages in the rudimentary vertebræ, into a *tube of primitive nervous substance*, the anterior part of which is expanded into three vesicles, placed at first one behind the other, but afterwards bent with the head and neck of the embryo, and named the *anterior, middle, and posterior, primary cerebral vesicles*; of these, the middle one is much the largest. From them are developed, respectively, the *prosencephalon*, the hinder part of which has been named the *diencephalon*, the *mesencephalon*, and the *epencephalon*, of which latter the hinder part is called the *metencephalon*. The tubular portion of this medullary canal, forms the *spinal cord*, which at first consists of numerous cells having a radiated arrangement around a central canal, and for a long time retains its hollow condition. Even in the perfectly-formed state, it presents a rudiment of this cavity, in the so-called *central canal of the spinal cord* (vol. i. p. 313). The cells next to the canal, form its epithelial lining, or *ependyma*, whilst the outer ones are developed into the nervous substance. The cord at first extends throughout the entire vertebral canal, but afterwards it grows in length less rapidly than the vertebral column, and the *cauda equina* is gradually formed. The substance of the embryonic spinal cord, is composed of simple nucleated cells, which are developed chiefly into the grey substance of the cord, but partly also into fine connective tissue and bloodvessels. The white substance of the cord is subsequently formed. The peripheral part of the spinal nervous system, as already mentioned, is developed, with the framework of the head, trunk, and limbs, from the middle germinal layer.

From the *posterior cerebral vesicle*, at first smaller, but soon larger, than the middle one, is evolved, in the *metencephalon* next to the spinal cord, the *medulla oblongata*. At

this point, the nervous substance, developed from the primitive medullary plates, does not form a complete canal, as in the spinal cord, but remains open behind, constituting the fourth ventricle, and is marked on its floor by the *calamus scriptorius*, which leads into the canal of the spinal cord. Anterior to the medulla, but still in the posterior cerebral vesicle or *epencephalon*, appear the *pons* and the *rudimentary cerebellum*, an angular projection forwards marking the line between them. At first, the cerebellum consists of a thin transverse plate of nervous substance; then it enlarges, and becomes laminated; the central part, or *vermiform process*, is recognised before the lateral parts, or *hemispheres*; the grey matter gradually becomes thicker on the surface, and the *corpora dentata* are formed within; the *pons Varolii* and the superior and inferior peduncles also gradually enlarge. Owing to the bend which occurs between the cephalic and cervical portion of the embryo, a posterior projecting angle is formed between the spinal cord and the posterior cerebral vesicle; this corresponds with the *cervical tuberosity* of the embryo.

The *middle cerebral vesicle*, or *mesencephalon*, slightly bent forwards and downwards across its middle, is, at first, the largest, but grows relatively slower than the others. After a time, it is developed, on its dorsal aspect, into the *corpora quadrigemina*, which form proportionally large masses, and are at first hollow—a condition which is permanent in Birds, but not in Mammalia. On the under-side, the *peduncles* of the cerebrum are formed; between these parts, a cavity remains, which ultimately shrinks into the small canal connecting the fourth ventricle with the middle ventricles of the brain, named the *aqueduct of Sylvius*.

The *anterior cerebral vesicle* is, at first, more prominent laterally, though smaller, than the middle one; it is also at first smooth, but soon exhibits a median sulcus, and grows far more rapidly than the others, being destined to form the *cerebrum*. It soon bends directly downwards. The portion immediately in front of the middle vesicle, named the *diencephalon*, forms the two *optic thalami*, which originally consist of a single hollow mass, but afterwards become solid; they are divided by a fissure, which remains as the *third ventricle*, and communicates behind with the Sylvian aqueduct. The *pineal gland* is either an offshoot from the thalami, or it is derived from the pia mater. The optic nerve also originates in a part of this vesicle. The pituitary body, or *hypophysis cerebri*, in both its nervous

part, and its posterior thyroid-like portion, is said to arise from the base of the brain, or to be in part developed from the pia mater. The *prosencephalon*, or portion of the anterior vesicle in front of the optic thalami, gives origin to the *corpora striata*, upon which the cerebral *hemispheres*, with the *corpus callosum*, the *fornix*, and the *ventricles*, are rapidly evolved. The *corpora striata*, and the *hemispheres*, are, it is said, at first separated by a slight constriction.

The *hemispheres* are developed from before backwards, leaving between them the cavity of the third and lateral ventricles, which, for a time, open freely into the yet hollow *corpora quadrigemina*. Gradually the *hemispheres* overlap the optic thalami, and then, in the higher Vertebrata, the *corpora quadrigemina*, and, lastly, even the cerebellum. At first smooth on the surface, and composed of thin walls enclosing a large cavity, the *hemispheres*, by degrees, become thicker, and marked on the surface with the *primary grooves* or *fissures*, which subdivide them into frontal, parietal, occipital, temporal, and central lobes, and afterwards with the *secondary sulci* between the *convolutions*—the grey matter on the surface also gradually becoming thicker. The cerebral *hemispheres*, developed on each side of the middle line, are first connected only at their *base* and *anterior part*, by rudimentary commissural structures of nervous substance: these are the commencing peduncles, which may be traced, as white bands, upwards from the cord, the anterior commissure, and the rudimentary transverse commissure or *corpus callosum*. But, as the *hemispheres* grow backwards, the transverse commissural fibres of the latter, extend in the same direction, and thus the future *corpus callosum* is formed with the *fornix*, composed of longitudinal fibres, beneath it, and the *septum lucidum*, enclosing the cavity of the fifth ventricle, between them. From the under-surface of the anterior part or frontal lobe of each hemisphere, a hollow process extends forward, forming the future *olfactory lobes*, the central cavities in which, in some animals, remain, in communication with the ventricles of the *hemispheres*, but, in others, are obliterated. From the hinder and lateral part of the anterior cerebral vesicle, the *primary optic* or *ocular vesicle*, or rudimentary eye, is developed, forming connections with the optic thalamus and *corpus quadrigeminum*. From both these latter parts, which are then hollow, two tubular processes of nervous substance, extend forward to the optic vesicles, and are ultimately developed into the optic tracts and optic

nerves. Farther back, on the sides of the future medulla oblongata, are the primary *auditory sacs* or vesicles, which are not developed, like the ocular vesicles, as outgrowths of the cerebral vesicles, but commence on the surface of the embryo, as will be immediately described.

The membranes of the brain and cord, are formed between the nervous centres and the walls of the cranial and spinal cavities. The pia mater is first recognisable.

The *sympathetic nervous system* is said to be developed from the middle germinal layer.

The Organs of the Senses.

The Nose.—As the olfactory lobes become consolidated, the nasal cavities, with the olfactory lining-membrane, are developed as inversions of the integument of the face, in the so-called primary olfactory groove. This, remaining open, becomes subdivided, to form the two nasal passages or fossæ. At one time, these fossæ are closed at the bottom, a condition which is permanent in Fishes; afterwards they communicate, in front of the palate, with the mouth, as in certain Amphibia; finally, they open only into the pharynx, as in Reptiles, Birds, and Mammals.

The Eye.—The *primary ocular* or *optic vesicles* commence, as already mentioned, as flask-shaped outgrowths of the first cerebral vesicle, with which they soon appear connected by a hollow stalk, the future optic tract and nerve. The interior of each optic vesicle, quickly becomes lined with nervous substance. At the same time, the surface of the common integument covering the vesicle, presents an inversion of the epidermic layer, which, becoming constricted at its orifice, closes and forms a sac; this is ultimately converted into the *capsule of the lens*, within which the lens-fibres are gradually developed, from radiating, epidermoid, nucleated cells. This growth, with other deeper tissues, pushes, as it were, the anterior and lower part of the nervous layer of the primary optic vesicle, upwards and inwards, against the posterior and upper part, giving rise to a cup-shaped nervous expansion, open below, named the *secondary optic vesicle*, within which the *vitreous humour* is developed, this being also, like the lens, an integumentary structure. The sides of this secondary vesicle, consist of two layers, which subsequently blend, and their edges, at first separated below, close in that situation, include the central artery of the

retina, and form the anterior part of the *optic nerve* and the retinal expansion. The anterior part of this secondary vesicle, corresponds with the *pars ciliaris* of the retina, and gives origin to no nervous elements. The yellow spot does not appear until after birth. The outer coats of the eyeball, or the *sclerotic* and *cornea*, are partly growths of the secondary vesicles, and partly derived from the neighbouring cutis. The *choroid coat*, also derived from the secondary vesicle, is at first adherent to the retina; the *iris*, growing at a later period from the margin of the choroid, forms an imperforate curtain, the central part of which, or *membrana pupillaris*, becomes transparent, then gradually loses its vessels, and finally disappears. The capsule of the lens is, for a time, invested by a vascular membrane, supplied by the central artery of the retina, and connected with the pupillary membrane and margin of the iris. The *aqueous humour* is secreted very late, the parts in front of the lens, previously touching each other. For a time, the eyeball is simply covered with the integument, but this rises up, above and below, into small crescentic folds, which become the future *eyelids*; these, for a time, cohere at their edges, and then separate.

The Ear.—The *auditory sacs* are not developed, like the optic vesicles, from the cerebral vesicles, but, like the lens and its capsule, from inversions of the common integument. They commence by a little pit or depression, which afterwards becomes completely shut off from the surface, and, receding, is eventually attached to the side of the medulla. This primitive auditory sac forms the *sac of the labyrinth*, with which the auditory nerve, an independent formation from the medulla oblongata, is soon connected. From the sac of the labyrinth, are gradually developed, the membranous *semicircular canals*, and the winding *cochlea*, with the fluids in those cavities. All these parts are at first straight processes, but afterwards become curved or spiral. The cavity of the *tympanum*, with its ossicles, the tympanic bone, and the auricle, are formed externally to the deeper parts, in connection with the pharynx and Eustachian tube, as will be described with the development of the face. The *osseous* walls, which afterwards invest the *labyrinth*, are formed from the primitive cartilage of the base of the cranium. The *mastoid* process is not hollowed out into large air-cells until after puberty. The *external meatus* and the *auricle* are outgrowths of the annular fibro-cartilage, which forms the tympanic bone. The auditory grey nervous centre arises, near the posterior pyramid and restiform body

of the medulla oblongata, as two masses, the outer one of which gradually moves backwards into the cerebellum itself. The auditory nerve consists of two portions, both of which become connected with these masses; but the anterior portion of the nerve, also joins the superior peduncle of the cerebellum, and even reaches the inferior vermiform process (L. Clarke).

The Parts of the Face.

The extension downwards of the lateral ventral plates of the embryo, which, opposite the trunk, form the sides of the hæmal cavity, occurs also beneath the cephalic part. Here, however, where the future face is developed, the hæmal cavity is imperfectly closed in at the sides; for these plates, with their covering and lining membranes from the external and internal, or epidermic and intestinal germinal layers, split, on each side, into *four processes* or *lobes*, with little clefts between them, forming the so-called *visceral* or *branchial arches*, and the *visceral* or *branchial clefts*. The term branchial is applied to these arches, because the permanent gills or branchiæ of the Fish, and the corresponding temporary gills of the Amphibia, are developed from homologous parts; but in the embryos of the Reptile, Bird, and Mammal, these arches give rise, through very early metamorphoses, to other organs. Within them, minute, but important vessels, as will be hereafter seen, are temporarily present. Gills are never developed on them, and they never exercise a respiratory function. In these three last-named Classes, the allantois, a part not present in Amphibia and Fishes, is the embryonic respiratory organ.

The first branchial cleft, above the first arch, sometimes named the *maxillary cleft*, forms the cavities of the mouth and nose; these are originally conjoined, but subsequently become separated, by the growth of the upper jaw, from the substance of the first arch, between the nasal cavities above, and the mouth below. The nasal walls and septum grow downwards from the cranium, whilst the upper jaw and palate are developed transversely from the face, to meet them. From the posterior part of the second branchial cleft, between the first and second branchial arches, are formed, the cavity of the tympanum, which at first contains soft connective tissue, the Eustachian tube, which is also at first filled with a similar tissue, the *membrana tympani*, and the external auditory meatus and its appendages. The auricle commences as a little ring around

the margin of the meatus. The third and fourth branchial clefts completely close up, and disappear very early.

Within the branchial arches, little cartilaginous plates are soon developed. From the upper edge of the first of these arches, a process is formed, named the *maxillary lobe*, from which the upper jaw is developed, together with the whole side of the face, including the internal pterygoid process and the palate-bone. The malar bones and lachrymal bones are formed as *opercular* bones. The first arch also gives origin, by another process, to the rudimentary *lower* jaw, and likewise, it is said, to the tongue. From the cranium, a median process, known as the *frontal process*, descends in the middle line of the face; and with this, an external and internal nasal process are also connected. These, by their junctions, form the walls and partition of the nasal fossæ, and the centre of the upper lip. In this latter part, the intermaxillary bones, which carry the upper incisor-teeth, are independent formations. The lachrymal duct is a fissure which remains partly open, between the external cranial nasal process and the facial maxillary lobe. Sometimes these parts are arrested in development, and fail to unite properly, giving rise to the conditions of *harelip* and *cleft palate*. Certain other congenital defects, connected chiefly with the apertures of the body, as well as with the back of the head and spine, are explained by similar arrests of normal adhesive processes of development.

From the middle part of the first branchial arch, to which we now return, the incus of the tympanum is developed. From it, also, a remarkable cartilaginous process, named *Meckel's process*, or *Meckel's cartilage*, arises, which gives origin to the *malleus*, and also extends forwards from that bone to the rudimentary lower jaw, which is developed independently upon it, after the manner of the opercular bones of the cranium, which rest upon the basal bones. Afterwards, Meckel's process wastes, except a part, which forms the *processus gracilis of the malleus*. From the second branchial arch, are developed the *stapes*, from a minute cartilage, and also the stapedius muscle, with its bony canal; these belong to the tympanic cavity. In the neck, the second arch forms the styloid process, the stylohyoid ligament, and the *little cornu* of the *hyoid* bone, which early unites with the tongue. The cartilage of the third branchial arch, gives origin to the *great cornu* and *body* of the *hyoid* bone; but the arytenoid cartilage, and the epiglottis, are developed from the first arch. The

fourth branchial arch soon coalesces with the side of the neck. All these changes occur very early in the pulmonated Vertebrata.

The Alimentary Canal.

The digestive canal is at first merely the interior of the body-cavity, which is formed by the folding downwards and inwards of the lateral ventral plates, and which, originally, communicates widely with the yolk-sac, by the open vitelline duct. The walls of this common body-cavity, are derived principally from the middle germinal layer, but they are lined by the inner or intestinal germinal layer. It is a short straight chamber, closed at both the cephalic and the caudal end of the embryo. Its innermost part soon separates from the sides of the embryo, and forms a tube, in which an abrupt *bend* occurs opposite the umbilical opening, and for a time projects through it, being there connected with the vitelline duct. In the Bird, this duct continues open, even after the chick is hatched; but in the Mammalian embryo, it soon becomes closed, and, attached to the primary bend of the alimentary canal, forms the slender *pedicle of the yolk-sac* or *umbilical vesicle*. The part of the canal, or tube, above the bend, forms the pharynx, œsophagus, stomach, and a portion of the small intestine; the part below the bend, the remainder of the small intestine, and the large intestine: the distinction between these, is soon indicated by the appearance of a cæcum, a little lower down than the bend. The closed upper end of this alimentary tube, extends to the base of the cranium, corresponding with the pharynx, the œsophagus being continuous with it below. The lower closed end corresponds with the lower portion of the rectum. At a certain time, there is neither an oral nor an anal aperture. The buccal orifice is originally formed by a depression above the first branchial arch, and then opens into the pharynx, the tongue being already developed in its interior. At the lower end of the rectum, the anal orifice appears as a depression, which ultimately opens into the bowel. The *stomach* proper is, at first, a longitudinal dilatation of the alimentary tube, which gradually assumes an oblique, and then a transverse, position. The primitive alimentary tube is closely attached to the vertebral column, and is covered by the peritonæum formed upon it and upon the walls of the cavity of the body, as it separates from the latter. But after the stomach has changed its position, the convolutions of the small intestine, and the remarkable bend of the large

intestine around them, occur. These changes are owing to a greater development of the intestine, than of the mesentery. This latter structure and the omenta are now fully formed. The small intestine is, for a time, wider than the large intestine. The vermiform appendix of the cæcum is, as it were, an incompletely developed, yet growing, part of the large intestine. The valvulæ conniventes of the small intestine and the sacculi of the colon, appear afterwards. Fringed villi, at first, exist throughout the embryonic alimentary canal, but they are permanent only in the small intestine.

The Teeth.

In the cavity of the mouth, the middle and internal germinal layers give origin to the buccal *papillæ* and also to the *teeth*, which are themselves formed, partly by the corium, and partly by the epithelium of the buccal mucous membrane. At first, the rudimentary upper and lower jawbones of Man, have no alveoli, and the membrane which covers their horse-shoe shaped borders, is quite smooth. After a time, however, a groove appears on the margin of each maxillary bone, which gradually deepens and widens, and becomes separated by thin osseous septa, into rudimentary alveoli.

In the meantime, according to one authority (Goodsir), the mucous membrane over the margin of the jaws, also presents a groove, called the *primitive dental groove*, from the bottom of which minute *papillæ* arise, in the human jaw ten in number, above and below. These are the rudimentary pulps of the future milk teeth. Those of the upper jaw appear first. In each, the order of their appearance, is as follows:—the first molar, the canine, the central incisor, the lateral incisor, and the second molar. This is the *papillary* stage, which is soon converted into the *follicular* stage, by the rising up of membranous folds, between and around the papillæ. By this time, each papilla has enlarged, and assumed the form of the crown of the future tooth; whilst small membranous lids, or opercula, corresponding, in number and shape, to the surfaces of each tooth, overlap the papilla. Subsequently these follicles become deeper, and are closed by the adhesion of their opercula and by the union of the borders of the dental groove, and, at their upper part, a thicker portion is seen, which constitutes the *enamel organ*. The so-called *dental sacs* are thus formed, and the *saccular* stage is completed.

According to Kölliker and others, however, the dental

papillæ, follicles, and sacs, are formed entirely beneath the epithelium over the jaw. The *enamel organ* is the part first developed, as a thickening of the deeper layers of the epithelium, which grows down into a flask-shaped depression, formed in the vascular layer or corium of the mucous membrane; the *papilla* then rises up as an extension from this membrane. By removing the epithelium, the dental groove, follicles, and opercula, of Goodsir, are seen.

The form of the summit of the *papilla* being completed within the sac, a thin *cap of dentine* appears on it, which gradually increases at its edges, and becomes thickened on its inner surface; whilst the papilla, at first growing wider, but then contracting at its base to form the *cervix* of the tooth, continues to grow longer, and commences to form the *fang*, which shortly acquires its covering of *crusta petrosa*. In the meantime, by a separate process, the surface of the cap of dentine, on the crown, becomes covered by the growing *enamel*, formed from the *enamel organ*. At last, by the gradual growth of the fang, the tooth is pressed against the gum, which, becoming absorbed, the finished surface of the enamel is exposed, and the tooth is *cut*. The fang is now completed to its point, and the papilla, now called the *pulp*, remains as a vascular and nervous mass, occupying the pulp cavity, and receiving its vessels and nerves through an orifice left at the apex. In the meantime, the alveolus in the bone, has closely adapted itself, to the fang.

In the growth of a tooth having *several* cusps and *fangs*, a separate shell of dentine and enamel forms on each cusp, the whole afterwards uniting; whilst the dentine shoots in at opposite points of the base of the pulp, where this begins to divide to form the separate fangs.

Behind the growing milk teeth, in each jaw, *recesses* are formed in the corium of the mucous membrane, which also become filled with epithelium, out of which future enamel organs are developed. Moreover, a vascular papilla arises from the bottom of these flask-shaped depressions or *cavities of reserve* (Goodsir), which finally close, and become the sacs of a like number of the permanent teeth. These sacs are at first oval, and adhere to the back of the sacs of the corresponding milk teeth, but afterwards they become more elongated, and recede from the gum, to which they are only attached by a fine cord or pedicle, found behind the necks of the other teeth. In this way, in Man, the ten anterior permanent teeth in each jaw, are developed. But the sacs for the three additional

or superadded permanent teeth, on each side of the two jaws, viz., the sacs of the permanent molars, are formed by little *posterior cavities of reserve*, which appear on the edges of the jaws, behind the other teeth. These latter teeth are cut like the milk teeth. But the anterior permanent teeth emerge differently. Between the fang of the temporary tooth and the sac of the corresponding permanent tooth, there is a thin layer of cancellated osseous tissue; and in this bone, is a little canal, which lodges the pedicle of the sac. The crown of a permanent tooth, being completed within its sac, its fang or fangs begin to be formed; the crown is pressed against the bony partition separating it from the fang of the milk tooth, and, when this is absorbed, against the fang itself. A peculiar, thick, pulpy, vascular areolar tissue intervenes between them, and appears to accomplish a gradual absorption, first of the crusta petrosa, afterwards of the dentine, and even of the lower part of the enamel of the milk tooth. Sometimes this process of absorption, which is not due merely to pressure, is temporarily interrupted, a renewed deposition of dentine taking place. At length, the side of the socket, the fang, neck, and even part of the crown of the milk tooth, having been absorbed, the tooth is loosened, hangs for a time by the gum, and finally drops out. The permanent tooth rises in its place; the crown appears above the gum, whilst the fang, closely followed by a consentaneous development and modelling of the osseous tissue of the jaw, becomes firmly fixed in its socket. The giving way and disappearance of the bone in one place, and its growth in other directions, by interstitial absorption and deposition, are remarkable examples of the plastic endowments of the osseous tissue.

The development of the teeth in the Mammalia, conforms generally, to the process above described.

The dentition of the Marsupialia, however, has lately been shown to be very peculiar. The only tooth which is successional, is the *last premolar*, on each side of both jaws; it alone is preceded by a temporary tooth, which has a molar shape. The other teeth of the Marsupial jaw, not having any predecessors, might perhaps be regarded as themselves belonging to the *first set*, though not falling out; but this view seems contrary to the homologies of these teeth, which show them to be permanent. Perhaps in a very early stage of development, transitory rudiments of other temporary teeth, may be met with in the fore part of the jaw of the Marsupials (Flower). The milk premolars of the guinea-pig, are shed even before birth; the milk teeth of the Bats, Insectivora, and seals are very simple and temporary; the first incisors of the

elephant are very small, and the large incisors of the Rodents, do not appear to have temporary predecessors.

The teeth are always parts of the *exo- or dermo-skeleton*. The replacement of the deciduous, by permanent teeth, occurs only once. But in the carnivorous Cetacea, the Edentata, and the Monotremata, there is no succession of teeth. Such animals are called Monophyodonts, the ordinary Mammalia being named Diphyodonts. The teeth of Reptiles and Fishes, are also developed upon papillæ, and are mostly enclosed in sacs, or follicles, in certain cases, provided with an enamel organ; in the parrot fish, the rudiments of the teeth sink into alveoli; in the pike, they sink only into sacs or follicles; in the sharks and rays, they remain as papillæ on the surface, thus representing the papillary, follicular, saccular, and alveolar stages of development of the teeth of Mammalia.

The Digestive Glands, the Lungs, and the Spleen.

The mucous glands of the mouth, the salivary glands, the mucous glands and special tubular glands of the stomach and intestine, the liver and pancreas, and even the lungs, are developed from the middle and innermost germinal layers, the latter forming the epithelial lining of the several glandular organs. They usually commence by processes of epithelium, which sink into the corium, penetrate into numerous bud-like projections, corresponding with the future lobes and lobules of the gland, and are subsequently hollowed out, to form the ducts.

Thus, the *lungs* commence by two solid cellular processes, from the front of the œsophagus, which soon become hollow. These processes branch out into numerous, at first solid, but afterwards hollow, ramifications, which become lined by a ciliated epithelium, and form the bronchi, bronchia and air-cells. The primitive lungs open separately into the pharynx, but afterwards by a common trachea. The trachea and larynx are produced by a lengthening out and excavation of a primitive peduncle, derived from the œsophageal walls: the larynx is developed from two lateral symmetrical masses of blastema, connected in front. Until the lungs are inflated at birth, they resemble a solid gland containing ducts with terminal acini; they then lie close to the back of the thorax.

The *liver* first appears, as two small conical projections of the corium and epithelial tissue, on the side of the intestine, below the stomach. These soon become hollow, and from them, numerous, solid, cylindrical branches extend into the growing matrix. Continuing to extend, these ramified masses of cells, ultimately unite in a terminal network, and, becoming

hollowed out, form the bile-ducts. The liver rapidly acquires a relatively large size, and is lobed; it soon even begins to secrete bile, or, at least, the colouring substance of the bile, for the biliary acids are said to be absent. This imperfect hepatic secretion enters the intestine of the embryo, forming the so-called *meconium*.

The *pancreas* is developed, in a similar manner, close to the spleen, by the formation of a small mass of cells from the epithelial layer on the left side of the intestine, which afterwards grows, and becomes canaliculated to form the pancreatic ducts.

The *spleen* commences near the great curvature of the stomach, but probably from a distinct blastodermic mass. The *thyroid* body appears as a similar small mass, in contact with the œsophageal lining membrane, in close connection with the commencing larynx. The *thymus* is said to originate *separately*, in front of the great vessels of the neck, as a delicate closed tube, which becomes diverticulated at the sides, and filled with nucleated cells and fluid.

The Urinary and Reproductive Organs.

The *bladder*, as already stated, is a part of the *urogenital sinus*, and is connected at its apex with the *urachus*, or obliterated abdominal portion of the allantois. It is developed originally, as a small pouch, connected with the lower end of the large intestine. The part of the intestine below the primitive communication with the bladder, forms a true *cloaca*, into which the digestive, urinary, and reproductive canals all open. The anterior part is soon separated from the proper intestinal portion, by a septum which corresponds with the future perinæum. It is this anterior part, which forms, for a time, the *sinus uro-genitalis*, the common outlet of the urinary and reproductive passages, and which becomes ultimately modified according to the sex.

Very early in embryo life, two remarkable symmetrical organs appear, at first as two linear elevations, one on each side of the primitive vertebræ, forming proportionally very large reddish masses, and reaching from opposite the heart to the lower end of the vertebral column. Originally, they consist of two symmetrical longitudinal canals, in the walls of which slight cæcal depressions speedily form. When fully developed, they consist of numerous comb-like, blind, hollow processes, lined with ciliated epithelium, very vascular, and communi-

cating each with a long duct, which runs downwards, and opens into the genito-urinary sinus. Malpighian bodies, or arterial tufts, have been detected in them. These organs are the *Wolffian bodies*, or *primordial kidneys*, so called because their secretion contains, amongst other products, uric acid; in Fishes, they are said to become the future kidneys. In the Warm-blooded Vertebrata, they are in no way connected with the development of the kidneys, but rather with the first formation of the reproductive organs. Their secretion finds its way, through the genito-urinary sinus, into the allantois, or future urinary bladder. They are proportionally larger in the lower Vertebrata, and persist for a longer time. At first, highly vascular, they afterwards almost entirely disappear, as the proper kidneys are formed. The kidneys themselves, commence as thick, smooth, or lobulated opaque masses, or processes of cells, arising from the sides of the cloaca, behind the Wolffian bodies; as these latter diminish, the kidneys enlarge, and gradually receding from the urogenital sinus and cloaca, assume their future normal position. They continue to be connected with the urogenital sinus, by a duct which forms the future *ureter*, *pelvis*, and *calyces*. The renal matrix at first contains bundles of solid processes, which afterwards become hollowed out, to form the tubuli uriniferi; these are said not to open originally into the pelvis of the kidney. The kidneys soon become lobulated, but afterwards smooth. Malpighian bodies appear in them very early. The supra-renal bodies are independent formations.

On the inner side, and somewhat behind each Wolffian body, appears, rather early, a little opaque mass, which is ultimately changed, according to the sex, into the *ovary* or the *spermatic gland*. Two ducts, the *ducts of Müller*, appear simultaneously, connected at their lower ends with the sinus uro-genitalis, but terminating at their upper ends, at first, in blind extremities. In the male, these become connected with the spermatic gland, at the back of which, even in the adult condition, they sometimes present a long diverticulum. In this situation, too, vestiges of the Wolffian bodies may still be traced (Giraldés). In the female, these ducts do not coalesce with the ovaries, but remain separate and form the oviducts of Fishes, Amphibia, Reptiles, and Birds, the left one only usually persisting in the adult condition, in the two last-named Classes. In the Mammalia, they constitute the free part of the Fallopian tube; between it and the ovary, are found, in the adult, vestiges of the Wolffian

bodies (Rosenmüller). From the lower end of these tubes, and from the portion of the genito-urinary sinus into which these ducts open, the future uterus, or the prostate gland, is developed. In the Monotremata, an intermediate condition exists, approaching to the birdlike structure of the parts; for the two Fallopian tubes open separately into the uro-genital sinus. In the Marsupials, and some Rodents, they combine before they open, forming a *double* uterus. In the Marsupials, remarkable pouches, the so-called *marsupia*, supported by special bones, are found in connection with the pelvic organs; they receive the young, which are born in an immature state. In other Rodents, the uterus is cleft. In the Cetacea, Solipeds, and Ruminants, the uterine chamber is double, or *two-horned*; in the Carnivora, Insectivora, and Cheiroptera, the horns of the uterus are comparatively short. In the apes, this organ is but slightly notched. The human uterus forms a simple triangular chamber.

The Heart, Bloodvessels, and Blood.

The first appearance of bloodvessels in the embryo and its appendages, can be best observed in the incubated hen's egg. In the middle germinal layer, where it extends over the yolk, linear clusters of nucleated cells appear, and arrange themselves in streaks, which soon unite in a retiform manner; these speedily become distinguished, by special processes of differentiation or development, into an external firmer part, or wall, which forms a future *bloodvessel*, and an internal softer part, which remains fluid, and further separates into liquor sanguinis and blood corpuscles, some of which are colourless, whilst others soon acquire the characteristic red colouring matter. The fluid central part of these red streaks, is blood; it soon exhibits movement, and, as the vessels become connected, it forms continuous streams. These earliest vessels on the surface of the yolk, constitute the so-called *vascular area*; they terminate in a marginal bloodvessel, known as the *sinus terminalis*; this, extending beyond the embryo, both in front and behind, divides into vessels which run towards each extremity of the embryo. In the meantime, in front of or beneath the chorda dorsalis, near the cephalic end of the embryo, within the middle germinal layer, a solid mass of cells appears, connected with certain branching streaks; the outer part of this becomes converted into an elongated sac or dilated tube, the primitive heart, and the interior into the

liquor sanguinis and blood corpuscles; whilst from the connected streaks, are developed, an arterial trunk which divides into two branches, at the anterior end of the now tubular heart, and a venous trunk communicating with its hinder end. These rudiments of a propulsive organ or heart, with its embryonic arterial and venous channels, are, moreover, soon connected with the vessels already mentioned as being formed outside the embryo, in the vascular area upon the yolk, and thus a determinate direction is given to the blood circulating through the embryo and the surrounding vascular area. At this time, there are no capillaries in the embryo; all the vessels are either arterial or venous. The blood appears to pass out from the sides of the embryo, and to reach the terminal sinus, by which it is conveyed back in the direction of the cephalic end of the embryo. The *heart*, which originates very early—after the commencement of the second day in the chick—in a group of cells connected with the intestinal portion of the middle blastodermic layer, soon forms a straight longitudinal *utricle*, or *sac*, from the anterior end of which a short arterial trunk arises, the *bulbus arteriosus*. This speedily divides into two branches, which give off two anterior and two posterior vertebral arteries; the former supply the cephalic part of the embryo, and the latter soon unite, to form the descending aorta. The primitive aorta is very early connected with two small arteries, named the *omphalo-mesenteric* or *meseraic* arteries, which pass laterally on to the yolk-sac, hence they are also named *vitelline arteries*, and branch out into the vascular area; they convey the blood from the heart and body of the embryo, over the yolk-sac. After a time, one of these arteries disappears, the left usually remaining. From the vascular area, the blood is returned to the embryo, by the anterior recurved ends of the *terminal sinus*, which appears to have the function of a vein. But from the hinder part of the vascular area, other veins proceed, and end in posterior branches, which join the recurved ends of the terminal sinus to form the two *omphalo-mesenteric veins*; these enter the embryo, and become connected with the posterior extremity of the still straight, sac-like, heart. After a time, the right omphalo-mesenteric vein shrinks, the left one remaining pervious.

In the Bird, the vessels of the vascular area become very large, and form the *vitelline vessels*; they send vascular processes into the substance of the yolk, and thus food is absorbed by, and supplied to, the embryo. The yolk-sac is the temporary

alimentary chamber of the embryo, and, in certain *lower* animals, it remains so; its vessels are represented by the abdominal veins in the Non-vertebrate forms. The vessels of the yolk persist in the Bird up to the period of hatching, and for some time afterwards, until the contents of the yolk sac are completely absorbed. But in the Mammalian ovum, the omphalo-mesenteric artery and vein continue very small, and soon become obliterated. The circulation through the vascular area to the terminal sinus, in them, is probably chiefly respiratory.

But now a change takes place in the circulation outside the embryo, both in the Bird and in the Mammal. The allantois grows, and two arteries, proceeding from the posterior vertebrals, named the hypogastric or umbilical arteries, proceed out upon it; whilst two veins, returning upon it, also named *umbilical*, join the common trunk of the omphalo-mesenteric veins. The right umbilical vein then disappears, and the left one, enlarging, as the single left omphalo-mesenteric vein diminishes, soon appears as the chief median vein, carrying the blood from the allantois, or its modification, the placenta, back to the heart of the embryo. It now passes through or beneath the liver. When the vitelline vessels, in the Mammalian embryo, have shrunk, the proximal part of the left omphalo-mesenteric vein, forms the trunk of the *portal* vein, and the part beyond this, after joining with the umbilical vein, constitutes the *ductus venosus*, with which vessels the liver and its veins are now seen to be connected.

As the embryo develops, the heart itself undergoes a process of bending or curvature, like an italic letter *S*. At the same time, it enlarges, and acquires thicker walls; the anterior or arterial part, which gives off the bulbus arteriosus, is now placed nearer to the under side of the embryo, whilst the posterior or venous part, which receives the conjoined veins, is turned backwards towards the vertebral column. The saccular *heart* is now marked off, by two constrictions, into *three chambers*, of which the first, or the one nearest the veins, soon exhibiting two superficial bulgings, corresponds with the *future auricles*; the second, also quickly showing an external line of subdivision, or notch, forms the *ventricles*, and the third, lying in front of and above the others, forms the bulbus arteriosus. Each of these quickly becomes subdivided. Thus, a *septum*, commencing on the anterior part, opposite to an external groove in its ventricular portion, grows upwards and backwards from the apex to the base of the heart, and ultimately

divides it into the *right* and *left* ventricles. Some time after this, the septum between the *auricles* begins to appear, growing both from above and below, like two folds with crescentic margins; the edge of the upper fold, as it grows, keeps to the right side of the lower fold, so that the passage from one auricle to the other, named the *foramen ovale*, is more or less oblique. The septum is completed at the period of hatching of the chick, and of the birth of the Mammalian embryo. Lastly, the bulbus arteriosus becomes subdivided longitudinally, into the pulmonary artery and the aorta, each remaining connected with its respective ventricle. The primitive heart, whilst it is still merely a straight tube, already manifests its proper function, its walls containing sarcoous cells of round, oval, and fusiform shape, and distinctly contractile, the contractions soon being seen to proceed, in regular succession, from the hinder, or vengous, to the anterior, or arterial end. Then, and even much later, when the heart is beginning to acquire its characteristic shape, its contractile walls present no distinct muscular fibres, but only large contractile nucleated cells, which are at first roundish, but afterwards become developed into spindle-shaped, or even forked, contractile fibre cells. The valves are developed, in their respective positions, from the inner surface of the heart, commencing very early.

The *arterial system* of the embryo, is developed by the formation, and subsequent metamorphoses, of five arches on each side, which are formed in succession from the original arterial trunk at the anterior end of the heart, all, however, not being present at the same time. The arch first formed, consisting of the two branches into which the primitive arterial trunk divides, and which, curling backwards, unite along a part of their course to form the descending aorta, has already been described. Behind this first arch, a second, third, fourth, and fifth arterial arch are formed on each side, the first arch being obliterated before the last one appears; all in turn coalesce as they pass backwards, like the returning part of the first pair, to assist in forming the descending aorta. This is the condition which persists in Fishes, by which the trunks of their characteristic branchial vessels are formed (p. 267). In the higher Vertebrata, this state is very rapidly changed, and its several phases of development correspond with the adult condition of the Amphibia. and, in some respects, of Reptiles and Birds as well. These changes fully explain the mode of origin of all these varieties, from a common Vertebrate embryonal

type. The upper primitive arterial arches, or primary arches, are said to occupy the third branchial or visceral arches or lobes, already described as appearing in the facial and cervical regions of the embryo. These arterial arches are thus modified:—The *fifth*, or *posterior* arch, the last one formed, disappears on the right side; whilst, on the left, it constitutes the trunk of the future pulmonary artery, and joins the fourth arch. This *fourth* arch, on the left side, forms the left aortic arch, which, joining with the first, then descends and unites, in the Bird, with the corresponding or fourth arch of the right side, to form the aorta; but in the Mammal, the fourth arch, on the right side, does not form a right aortic arch, but remains pervious, as the innominate and the commencement of the right subclavian arteries, from which the vertebral and axillary arteries are given off. On the left side, the subclavian is given off directly from the fourth, or left aortic, arch. The commencement or inner ends of the *third* arches, form the corresponding common carotids, whilst the third arches themselves remain as the internal carotids. The commencement or inner ends of the first and second arches, become the external carotids, the transverse parts of the last-named arches, entirely disappearing (Rathkè).

The *veins* of the embryo, consist, at first, of four symmetrical *cardinal veins*, two anterior and two posterior, one on each side. The anterior and posterior vein of each side, join to form the so-called right and left *ducts of Cuvier*; these again unite in the middle line, into a very short trunk, which, at an early period, opens into the single auricle, and, except in Fishes, ultimately forms part of that cavity; hence the two ducts of Cuvier open independently, as two superior venæ cavæ, into the auricle. This condition remains permanent in Birds and some of the lower Mammalia, which possess both a right and a left vena cava superior, opening separately into the right auricle. Instances are occasionally met with, from arrest of development, of two such veins in the human body. The anterior cardinal veins remain on each side, as the internal jugular vein. Between them, across the root of the neck, a transverse branch is very early formed, below the future subclavian veins. This cross branch, becoming enlarged, at the same time that the part of the left cardinal vein, extending below it down to the coronary veins on the back of the heart, is obliterated, conveys the blood from the left side of the head and upper limb, over to the venous trunk of the right side, and forms the future

left innominate vein, the persistent venous trunk of the right side becoming the *vena cava superior*. The posterior cardinal veins originally return the blood from the Wolffian bodies, and from the hinder part of the embryo. These afterwards become the *azygos* veins, of which, however, the right one only remains in Man and the higher Mammalia, the left vein disappearing up to the back of the heart. Here, however, traces of the left cardinal *trunk*, or left *vena cava superior*, remain as the *cardiac sinus*, or the short dilated terminal portion of the great cardiac or coronary vein. Sometimes a smaller *azygos* vein, on the left side, ascending to the innominate, represents another portion of the primitive cardinal vein; from this point, however, down to the cardiac sinus, at the back of the heart, vestiges of the course of the primitive vein, may be found throughout life. The left superior *vena cava*, when it exists, pursues the same course. The inferior *vena cava* is developed as a median vein accompanying the aorta, altogether independently of the posterior *lateral* cardinal veins. It is chiefly formed by the upper part of the omphalo-mesenteric trunk, which is joined by the umbilical vein, forming the ductus venosus; it also receives the common trunk of the future iliac veins. It terminates, at first, in the left half of the common auricle, but is soon shut off from that, by the lower fold of the inter-auricular septum. The mode in which the pulmonary veins are formed, and brought into relation with the left auricle, is not known.

Embryonal and Fœtal Circulations.

The circulation established between the early embryo and the vascular area upon the yolk, has been called the *first embryonal* circulation; it is intended for nutrient and respiratory purposes. In the ovum of all the Vertebrata, it soon ceases to be sufficient as a respiratory circulation. Thus, in the Fish and Amphibia, the branchial arches give origin to external or internal gills, which carry on the embryonic respiration; but in the Reptile, Bird, and Mammal, the allantoic sac is developed, the bloodvessels of which convey blood outwards from the body of the embryo, in order that it may be aerated, and then return it to the embryo again, thus assisting in the respiratory function. Moreover, in the Mammalian ovum, in which the yolk is so minute, the allantois and its vessels, as we have seen, assist in the formation of the *placenta*, which is not only a respiratory, but a nutrient organ. This *allantoic*

or *placental* circulation constitutes what has been called the *second embryonal circulation*. It is thus carried on:—from the iliac arteries of the embryo, the two *hypogastric* or *umbilical* arteries proceed outwards along the allantoïd sac, and, in the eggs of the Reptile and Bird, ramify in the outer layer of the allantois, immediately beneath the permeable shell and shell-membrane. In the Mammalian embryo, the blood enters the membranous or villous placenta, and is returned by the single *umbilical vein*, which runs beneath the liver and joins the inferior vena cava, just below the heart. In passing beneath the liver, the umbilical vein communicates freely with the portal vein. The blood brought back by the umbilical vein, is *arterialised*; it partly enters the liver through its portal veins, and is thence returned by the hepatic veins, to the inferior vena cava, but it is partly conducted on directly to this-last named vein, the portion of the venous trunk which so conducts the blood, being named the *ductus venosus*. In the vena cava inferior, this mixed hepatic and arterial blood becomes further mingled with the venous blood from the hinder part of the embryo, and the combined stream then enters the right auricle, and here, guided by the Eustachian valve, is chiefly, and, in the early stages of development, entirely, conveyed, through the foramen ovale in the auricular septum, directly into the left auricle. On the other hand, the purely venous blood returned from the anterior half of the embryo by the superior vena cava, separated by the same valve, remains in the right auricle. The contents of the auricles being, by their contraction, driven into the corresponding ventricles, it follows that the partially arterialised blood in the left auricle, enters the left ventricle, and from it, is propelled into the aorta and its branches, whilst the venous blood in the right auricle, enters the right ventricle, and from it, is propelled into the pulmonary artery. The pulmonary artery is, in the embryo, connected by a short arterial trunk, named the *ductus arteriosus*, with the under side of the arch of the aorta. Hence the blood in the descending aorta below that point, is mixed with the venous blood collected in the right auricle, whilst the arch of the aorta contains the arterialised blood collected in the left auricle. This latter blood is therefore conveyed by the great branches given off from the arch of the aorta, to the anterior part of the embryo, *i.e.* to the head, neck, and upper limbs; whilst the former, or non-arterialised blood, proceeds, in very small quantity, through the

still narrow pulmonary artery, into the collapsed lungs, but almost entirely through the descending aorta, iliac arteries and their branches, to the posterior part of the trunk of the embryo and the hinder limbs. A portion of it, however, is also conveyed, along the hypogastric or umbilical arteries, to the allantois or placenta, to be once more renovated; from these parts it is then returned to the embryo, by the umbilical vein, as arterialised blood, and pursues the course already described, over again. The fœtal circulation is, therefore, largely accomplished by the action of the right ventricle, and the walls of this cavity, before birth, are of equal thickness with those of the left ventricle. The right auricle is then also larger and thicker than the left.

It is probable that, from the admixture of the venous blood of the embryo, at several points, with the arterialised blood brought from the allantois or placenta, no portion of the embryo is supplied with pure arterial blood, especially whilst the foramen ovale, between the auricles, is very patent. Nevertheless, the head and upper limbs always receive blood more perfectly oxygenated than that distributed to the lower half of the body. This difference is associated with the more rapid development of the important parts situated in the anterior half of the embryo. Thus, the head, the encephalon and the organs of the senses, exhibit a far greater activity of development, than the hinder portion of the embryo and the corresponding part of the nervous axis. The anterior limbs also show a greater relative development than the posterior. These conditions have even been regarded as having the relation of cause and effect; but probably they are merely associated conditions. As the heart approaches its perfect state, and the foramen ovale becomes smaller, and its course through the auricular septum more oblique, the arterialised blood is probably more completely conducted into the left auricle, and so, through the left ventricle, aorta, and great arteries, reaches more especially the anterior part of the body.

Change in the Circulation at Birth.

At the period when the young Reptile escapes from its egg, when the young Bird first chips the shell, and when the young Mammal is born, each begins to respire by the lungs. A modification of the circulation then becomes necessary, to connect it with, and adapt it to the newly-employed respiratory organs: the allantoid or placental circulations become arrested; the

allantois is withered, and the placenta is first detached from the maternal system, and afterwards from the young animal, near the umbilicus or navel. From the umbilicus inwards, the umbilical vein shrinks on its coagulated contents, as far as the portal vein, and forms the future *round ligament* of the liver. From the portal vein to the inferior vena cava, the venous channel, called the *ductus venosus*, likewise contracts on its coagulated blood, and is then obliterated, remaining only as a fibrous cord. The foramen ovale in the auricular septum, becomes completely closed. The ductus arteriosus, connecting the pulmonary artery with the arch of the aorta, the primitive *ductus Botalli*, also contracts on its coagulated contents, and is soon converted into a fibrous cord; whilst the right and left divisions of the pulmonary artery leading to the lungs, become enlarged, and convey a far larger quantity of blood than before; the pulmonary veins, which bring back the blood from the lungs to the left auricle, are, at the same time, proportionally enlarged. Lastly, the portions of the hypogastric arteries which pass upwards by the sides of the bladder and urachus, to issue at the umbilicus as the umbilical arteries, likewise shrink and become obliterated. By these changes, which are accomplished within three or four days, the circulation acquires its permanent condition, or what is called the *complete double circulation*; the venous blood, returned from the whole body, is propelled by the right auricle, exclusively into the right ventricle, and from thence, through the pulmonary artery and its right and left branches, entirely into the lungs. From these, it is returned, arterialised, to the left auricle, is exclusively delivered into the left ventricle, and is thence propelled through the ascending and descending aorta and their branches, on to every part of the body. To complete these changes, the left ventricle, which now performs the whole work of the systemic circulation, speedily acquires a greater thickness of its walls than the right ventricle.

DEVELOPMENT OF THE TISSUES.

Animal and Vegetable Cells.

Whilst the forms and relations of the organs, are evolved in the manner just detailed, their component tissues are undergoing development. These tissues, with their complex structure and composition, are gradually produced from simple, and originally identical, anatomical elements. They commence,

like the organs which they build up, in the early periods of the formation of the embryo, originating directly from, or through the agency of, nucleated cells of the blastoderm, held together by an intermediate *matrix* or *blastema* (βλαστος, blastos, a germ). These cells are themselves the internal offspring of the contents of two cells—the germ cell and the sperm cell. The former, or nidal cell, fertilised by the latter, produces a brood of uniform cells, from which, by further multiplication and differentiation, all the tissues are evolved. These two cells are, originally, elementary histological parts of the tissues of parent animals, evolved by special developmental processes.

It is supposed by Schleiden, Schwann, and their followers, that all organised tissues, whether animal or vegetable, are produced directly from cells; but, though this is proved concerning the vegetable tissues, there are certain animal structures, which, it would seem, are not formed out of such cells themselves, but are developed, for example, from the intercellular matrix or substance. Hence the so-called cell theory is regarded, by many, as exploded, so far as animal organisms are concerned. But if the definition of the term *cell*, be extended, these discrepancies of view, may be generally reconciled.

In a perfect vegetable cell, figs. 46, 47, as seen detached in the vesicle of a microscopic fungus, or aggregated in the section of an onion, there is found, a wall or *periplast* always composed of cellulose or lignin, with a contained *protoplasm* or *endoplast*, the outer part of which is often firmer than the interior, and is named the *primordial utricle*; in the endoplast, is a *nucleus*, and in that, often, a *nucleolus*; around the nucleus, is collected a soft, granular, *germinal matter*. In becoming *altered*, so as to constitute a vegetable tissue, these cells enlarge, change their shape, the nature of their walls or contents, and their connections or modes of junction, forming flat polygonal cells, polyhedral cells, elongated, fusiform, tubular, or reticular tubular tissue, plain, dotted, or spiral ducts, woody fibre, spores, zoosperms, pollen, or ovules. The intercellular substance is always scanty. For the formation of the tissue of a growing plant, such cells must also *multiply*; and this is effected by division of the cells, or by the formation of buds, or offshoots, which is much the same process, and resembles the fission or gemmation of non-sexual reproduction; but they can also multiply, as in the spore cases of fungi, by internal or endogenous formation, which more resembles the sexual mode of reproduction. In the vegetable cell, the essential punctum or point, the centre of nutritive or developing force, is the nucleus, or the nucleolus. It is this which appears to attract materials for the formation of the germinal matter around it, for the maintenance of the endoplast, and for the deposition of the periplast.

In animal cells, far greater variety of form and plasticity

of function, are observed. When in their most complete condition, as in the ovum, they consist, like a vegetable cell, of a cell wall or envelope, the *periplast*, of fluid or semifluid contents, the *endoplast*, of a *nucleus*, and usually of one, two, or more *nucleoli*. The cell wall is a thin, delicate, homogeneous, transparent membrane; but this is absent in many cells, such as the primary embryonic cells, and the white corpuscles of the blood, lymph, and chyle. The outer part of the endoplast, is said sometimes to be firmer than the rest, and to constitute a special investment, like the primordial utricle of the vegetable cell (Huxley). In less perfect cells, there is often merely found a nucleus enveloped in a soft granular mass, as in the fusiform, unstriped muscle cell. The perfect cells may be called *cystoplasts*; the imperfect cells, *gymnoplasts*. The cell contents of the former, or the cell substance of the latter, present, in certain cases, as in the primitive embryonic cells and in all newly-formed cells, besides fat particles, a peculiar semifluid, transparent, tenacious, albuminoid substance, called the *protoplasm*, which contains very minute molecules, and oleoid, and often amyloid matter. This protoplasm frequently presents movements, seen also in vegetable cells, which may depend on a contractility in the protoplasm, for it has been observed to be excited by electrical currents (vol. i. p. 182). This protoplasm usually diminishes, becomes altered, or disappears as the cell grows; but sometimes it is retained during its whole existence. It is very easily coloured by carmine, and is thus made evident in microscopic investigations. The soft substance which gathers especially around the nucleus, corresponds with the *germinal matter* of Beale, which he regards as the *formative matter* of the cell, as distinguished from the special contents, or investments, which he names *formed matter*. The nucleus is a vesicular body, which, in a growing cell, is round or oval; its nucleolus is also, by some, said to be vesicular, but it may be, for a time at least, solid. These two structures are the essential parts, the essential *puncta* of the cell, the so-called germinal centres, or centres of cell-nutrition and cell-life.

It is supposed by Schwann, that an animal cell may arise in the soft, clear substance known as *blastema*, a sort of *germinal matter*; that in this, by the development and collection of a number of minute molecules, a *nucleus*, called by him a *cytoblast*, is formed; and, lastly, that upon this, a fine membrane grows, and gradually separating itself from the nucleus, forms the cell wall, with its intermediate cell contents. This mode

of origin is also supposed by Schwann, to be the one by which new cells continue to be formed during the whole of life; but it is more commonly believed, that the nuclei of new cells, proceed from the division or multiplication of pre-existing cells, and that all are the direct descendants of those originally formed in the ovum. The hypothesis of the *free* formation of cells, is, as regards tissue life, the analogue of spontaneous generation, as regards animals themselves.

The formation of new animal cells from pre-existing cells, may take place in several ways. Thus the old or parent cell may divide into two cells; in this case, the nucleus first separates into two, and the cell itself then presents an indentation across its centre, which, gradually increasing, divides it into two cells, each containing its proper nucleus; or sometimes the nucleus, instead of dividing into two, may divide into three, four, or, as has been noticed in the embryo of the frog, even into six nuclei, the cell itself then separating into a corresponding number of cells. This has been named the *fissiparous* mode of development. In the so-called *gemmiparous* development, new cells are described as being formed by the evolution, and subsequent detachment, of buds from the side of a cell. Instances occur, as in the soft medullary tissue in the interior of bones, and also, it is said, in the spleen, of the formation, by repeated subdivision, of many nuclei in the interior of a single parent cell. In bone, these multiple nuclei of the cells, remain as nuclei; but in the spleen, they may develop into an ordinary nucleated cell. *Free* nuclei are those which are *found* in a blastema or matrix, in very actively growing parts, or in morbid new growths; they originate from, or by the influence of, the old or pre-existing nuclei of the surrounding tissues, themselves the progeny of still anterior cells. They may appear to be evolved, in some way, from aggregations of protoplasm, but still, it is submitted, always under the influence of preformed nuclei or nucleoli. In the so-called *exogenous* development, rupture of the wall of the old cell occurs, the nuclei escape, and a new cell is developed from each (Bennett). The *endogenous* mode of formation consists in an increase in size of the old cell, a cleavage of the nucleus into two, and the development of two cells within the original cell wall.

Animal cells undergo various changes in size and form (fig. 122). Their nuclei, for example, may increase in size and alter in shape, but not to such an extent as the cells them-

selves; in many cells, they become obscure; and in some cells, as in those of elastic tissue, they finally disappear. Their envelopes may expand and burst, or they may shrivel up and dry. The cells may dissolve and disappear, or become

Fig. 122.

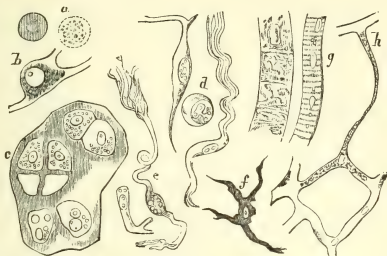


Fig. 122. Forms of animal nucleated cells. *a*, flat and round cell of red and white blood corpuscle. *b*, ramified cell of grey nervous matter. *c*, cells, multiplying by binary division of nucleus and cell, and embedded in a solid matrix of cartilage. *d*, cells of areolar connective tissue, showing their splitting into fibrillæ. *e*, elastic fibre cells. *f*, ramified pigment cell. *g*, muscular fibres. *h*, capillary vessel.

the seat of special deposits. Sometimes the substance of a cell undergoes but little apparent change; but usually, their contents are modified according to the tissue which they form, or the secretion which they prepare, *a*, *b*. Thus, some cells, as those of bone, dentine, and enamel, become loaded with earthy matter; others, as the red corpuscles, with iron in combination, and colouring substance; others, as those of adipose tissue, with fat; some with mucus or horny matter. Their relations to each other, may undergo many modifications. In the fluids of the body, as, *e.g.* the blood, the cells remain separate. In the solid tissues, they may be simply connected together by a minute quantity of intercellular substance, as in the epithelium and epidermis. Sometimes they elongate, and form fibres in various ways, *d*; or, after lengthening, they may subsequently join with similar cells, and give rise to the formation of tubes. The septa between these may be absorbed, and the coalesced and arborescent branches of different hollowed cells, may lead to the production of capillary, *h*, or lymphatic plexuses. Moreover, animal cells seem to exercise a singular power over the intercellular substance, blastema or matrix, which often

appears very large in quantity, in proportion to the cells themselves, as, for example, in cartilage, *c.* This matrix may be watery, soft and gelatinous, firmer and tenacious, still more solid and hyaline, or hard and opaque. It presents great varieties in chemical composition. It may be structureless, striated, fibrillated, fibrous, distinctly granular, or organically crystalline. Lastly, cells may undergo atrophy, or degenerate, become the seat of morbid deposits, especially of fat, and may finally die.

In contrasting the animal with the vegetable cell, it may be said that each vegetable cell, always a cystoplast, retains its own cell wall, and is, in a certain sense, independent of the rest. The intermediate substance is either absent or invisible, or it takes the form of a separate periplast for every cell. Each cell is encased anatomically, and isolated physiologically. They cohere rather than co-operate.

As to the animal cells, they are sometimes cystoplasts, often gymnoplasts. The presence of a separate periplast, is not universal; the endoplast probably has not even a primordial utricle; the outlying region of the cell, is not specially protected, but the intermediate matrix, which may be a common periplast, is most abundant, and often curiously specialised in structure and composition. The cells are fused together rather than coherent, and they manifest great dependence on each other, less individual isolation of function, and more marked physiological co-operation.

Nevertheless, both animal and vegetable cells are organic bodies, living by the properties operating in their centres of growth and nutrition, the nucleus or nucleolus. The vegetable cell feeds upon inorganic materials, the animal cell on a pabulum of organic origin, but not on an organised pabulum. Organisation only exists when, under the influence of nuclear, nucleolar, or cell action, the nutrient pabulum forms part of a living cell or its contents.

Development of the several Tissues.

Connective Tissue, and its varieties, areolar, fibrous, and jelly-like.

The embryonal connective tissue is a jelly-like substance, consisting of a transparent, soft amorphous matrix, in which numerous nucleated cell-elements are found. According to one view, some of these cells elongate in the soft matrix, become fusiform, unite into long wavy bands, and then split into the fibrillæ of the fibrous or areolar forms of connective

tissue, their nuclei being ultimately lost sight of. According to another explanation, the elongated cells and the matrix, blend together into a homogeneous mass, which then becomes fibrillated, fig. 122, *d*. In any case, the nuclei remain as *connective tissue corpuscles*. In many situations, softish and nearly homogeneous tissues are met with, which are evidently modifications or arrested developments of connective tissue, as in the coats of small vessels, in the soft neurilemma of the smallest branches of nerves, in the submucous coat and villi of the small intestine, in the papillæ of the skin, and elsewhere. The cornea presents a peculiar form of fibrous connective tissue; whilst the vitreous humour is an imperfectly developed areolar tissue, in which the cells have gradually disappeared, or exist only at the surface, whilst the matrix has become deliquescent. The soft embryonal connective tissue and the vitreous humour, contain no gelatin, but merely albumen and mucin. The chemical change into gelatin, occurs only with the perfect development of this tissue. The cornea contains chondrin and not gelatin.

Elastic Tissue.

In the development of this tissue, which is nearly always associated, or intermixed, with the connective, some of the cells of the embryonal tissue pass through the changes just described as proper to connective tissue cells, whilst others subsequently become much elongated and attenuated, branch out into fine ramifications, which unite with those of adjacent cells, undergoing similar changes, and preserve their nuclei in their central or thickest part. Sometimes these nuclei are ramified, at other times, they are fusiform. In many situations, as in fibrous membranes, ligaments, and tendons, in the true skin, in the cornea of the eye, and elsewhere, these ramified and united cells remain in the above described condition, their nuclei forming the connective tissue corpuscles. It has been said, that they are hollow, and that their fine ramifications convey a nutrient plasma through the dense fibrous tissues in which they lie, and hence these have also been called *plasm-cells*. Lastly, they have been said to form the commencements of the lymphatics; but this is not proved. According to some, the intercellular substance becomes fibrillated, and appears to be a sort of deposit from, or an excretion upon, the nuclei or cells.

In other situations, as in the loose areolar connective tissue, these fine fibres appear darker, and form networks of elastic fibres. These reticular fibres, becoming thickened by a deposit on their outer surface, form the stronger varieties of elastic tissue; by being joined or further thickened in parallel planes, they give rise to the elastic fibrous networks of the air-tubes, or to flat fenestrated elastic membranes, as in the arteries. The true elastic fibres are said to lose their nuclei; but they may be merely covered in and hidden.

Adipose Tissue.

The vesicles of this tissue, however small or large, are obviously nucleated cells, in which fatty matter has accumulated; their nuclei become obscured, or even disappear. The fat cells have been traced in all stages of development, from minute cells lying in the embryonal connective tissue, at first containing only an albuminous fluid, then a few

scattered oil-drops, and finally attaining their fully distended condition. Other cells adjacent to them, become changed into areolar connective tissue, bloodvessels, or lymphatics, which hold the fat cells together, and minister to their nutrition. Often, when the fatty matter is absorbed from the cells, in emaciation, the nuclei again become visible. In the marrow of bones, the nucleated cell structure is very clearly and beautifully seen. The reddish parts of the marrow, also contain smaller cells, and often compound nuclear cells, not fatty, called the *medullary cells*; these are very numerous in growing bone.

Cartilage, Fibro-Cartilage, and Yellow Cartilage.

The development of *cartilage*, is more easily traceable than that of any other tissue, from nucleated cells which are the immediate descendants of the primitive embryonal cells. In the simplest form of cartilage, as in the *chorda dorsalis*, and in certain other embryonal cartilages, the cells have very delicate walls, which are closely applied together, grow into a polyhedral shape, and present at first no appreciable intermediate matrix. More commonly, as in the cartilaginous pieces which precede the formation of the bones, and in articular cartilage, the original delicate cell-walls acquire an outer deposit or secondary cell-wall, which goes on thickening, blends with that of other cells, and also with a surrounding intermediate matrix. This is partly formed by the secondary membranes, but partly, it is said, in the blastema between the cells. This matrix either remains transparent, or becomes granular, or even more or less fibrillated. The cells themselves enlarge, and new ones arise *within* them, by successive endogenous binary subdivisions of the nucleus, accompanied by corresponding constrictions of the cell itself. Moreover, secondary capsules are formed around each new cell, whilst the capsule of the parent cell is fused with the intercellular matrix, and so disappears, fig. 122, c. The secondary capsules of the new cells, in their turn, blend with the matrix, and cease to be visible, whilst fresh formations of still newer cells, arise by division of their nuclei. The matrix thus formed, is apparently homogeneous, but exhibits faint striæ on the application of reagents. Sometimes a nucleus, instead of dividing, and each new one forming a separate capsule, becomes invested by a series of concentric capsules, developed one within the other. Sometimes no secondary capsules are formed, the primary one only persisting. The contents of the growing cells, become clearer, and the nucleus plainer. Amyloid substance has been found in young cartilage cells.

In *fibro-cartilage*, the intermediate matrix, with some of the cells, becomes changed into connective tissue, whilst other cells remain in the form of cartilage cells. In the *yellow* cartilages, intermediate elastic tissue fibres are developed between the cells, the rest of the matrix preserving its cartilaginous character.

Osseous Tissue, and the Bones.

The mode of formation of perfect bone, is exceedingly complex. It is never developed directly, but by the intervention either of *cartilage*, or of an imperfectly formed *fibrous connective* tissue, the *precursory tissues*, as they are called, in which *ossification* takes place.

In the *intra-cartilaginous* mode of origin of bone, the cartilage cells

first rapidly multiply, by the formation of new cells within the old ones, giving rise to clusters of softish nucleated cells in a clear matrix. In a long bone, these cells are largest in the centre, and have their long diameter across the axis of the bone; as they grow, the matrix usually becomes faintly fibrillated. Wherever ossification is about to begin, there appear in the cartilage-substance, certain soft ramified spots, which consist of masses of smaller nucleated cells, out of which the bloodvessels and blood are formed, these ramified soft spots coalescing, form canals, whilst the contained bloodvessels, establishing communications with previously existing ones, supply blood to the cartilage about to undergo ossification. The cartilage cells are first grouped into elongated clusters, separated by a clear matrix; a deposition of earthy matter then takes place in this matrix between the cells, in the form of opaque granules, by which process, the matrix becomes darker by transmitted light, and is soon calcified. This calcifying process partially affects the outer walls or secondary membranes of the cells, but not their contents.

The cartilage which is thus changed into bone, is called *cartilage of ossification*, *ossifying cartilage*, or *precursory cartilage*. The bony tissue into which it is converted, is called the *primary bone*; for it is no sooner formed than, as a general rule, it begins to be the seat of further important changes, during which it is almost entirely, or entirely, absorbed, to make way for the development of the *secondary bone*, or *perfect osseous tissue*. This last alone possesses lacunæ and canaliculi, concentric laminæ, Haversian canals, and their contained bloodvessels, cancelli, and in the case of the long bones, a central medullary cavity, with its vascular and medullary contents.

The change is thus accomplished. The primary bone is comparatively compact and opaque. In it, softer spots, or *areolæ*, appear, the *secondary cavities*, or *medullary spaces* (Müller), quite distinct from the ramified vascular canals in the precursory cartilage. These spaces appear to be formed by the junction of the adjacent clusters of cartilage cells, now disappearing, in consequence of the solution and absorption of the intermediate, dark, granular and calcified matrix. These areolæ contain, at first, a softish *ossifying blastema*, in which there very soon appear certain fresh nucleated cells, smaller than cartilage cells, and resembling *medullary cells*; besides these, there are developed, an imperfectly formed fibrous connective tissue and, likewise, many newly evolved bloodvessels. The adjacent areolæ being opened into each other, by the progressive absorption of the primary bone, their vessels become connected; and in their thinned walls, the secondary or perfect bone is deposited, in successive layers, by the transformation of corresponding strata of the soft ossifying blastema and its contained cells. Hence the explanation of the concentric laminæ of the perfect bone. The indistinctly fibrous matrix of the ossifying blastema, also becomes saturated with coalescing osseous granules, so as to appear perfectly transparent and homogeneous, instead of opaque and granular, like the primary bone. The entangled nucleated cells, the walls of which also become calcified, are believed to be converted into stellate cavities, by the partial intrusion of the calcifying process into them, and so to form the greater part of, or all, the bone *lacunæ*, whilst their radiating branches, multiplying, become very fine,

and joining those of adjacent cells, form the *canaliculi*. The primary opaque granular bone contains no lacunæ. Some of the areolæ, or spots of solution, absorption, and new deposit, reduced in size by the successive formation of concentric laminae of secondary bone around them, ultimately constitute certain of the Haversian canals; whilst others, even after they are lined by secondary bone, continue to widen by further solution and absorption of the surrounding bone, whether primary or secondary, and so form the larger nutrient foramina and canals, the small and large cancelli, and even the chief medullary cavity of a long bone. Indeed, so long as the bones themselves continue to grow, and even, but less evidently, throughout life, such processes of solution, absorption and re-deposit are repeated, in the secondary bone, over and over again, as it is modified, by age, in size, form, and structure.

In the *intra-membranous* mode of origin of bone, there first appears, in connection with some previously developed fibrous membrane or *precursory membrane*, which afterwards forms the fibrous *periosteum*, a soft *matrix*, or *blastema*, which contains largish nucleated granular corpuscles, and soon puts on an indistinctly fibrous aspect; it resembles, indeed, imperfectly developed fibrous connective tissue. This fibrous matrix and the walls of its included cells, become opaque by granular calcification. This occurring in successive strata, forms the *bone tissue*; whilst the cavities of the cells, becoming stellate, with fine radiating and communicating branches, constitute the *lacunæ* and *canaliculi*. This process of calcification occurs from the first, in a reticular manner. The fine spicula of the network, increase in thickness, by the formation around them, of a soft transparent *ostio-genic* substance (Müller), which ultimately becomes bone. The granular corpuscles, or *osteoblasts*, are embedded in the new-formed bone. The interspaces, meshes, or areolæ, form softer spots, the constituent cells of which develop into blood-cells, bloodvessels, and areolar tissue, and, after changes in their parietes, such as those already described in speaking of the secondary bone tissue of bones preceded by precursory cartilage and primary bone, constitute the canals of Havers, the larger vascular foramina and canals, and the cancelli of the cancellated bony tissue.

Although, therefore, the intra-cartilaginous and intra-membranous modes of formation of bone, differ from each other, the development of the secondary bone which goes on, *pari passu*, with the absorption of the primary cartilage-formed bone, is analogous to the intra-membranous mode of ossification. The soft ossifying blastema, in the one case, and the precursory membrane in the other, alike resemble an imperfectly formed fibrous connective tissue, and undergo similar changes. Chemical considerations also support this analogy, for, on removing the earthy matter from primary bone, its organic substance yields *chondrin*, whilst the animal basis of the secondary bone, and of the intra-membranous-formed bone, gives *gelatin* on being boiled.

The intra-membranous mode of ossification, is solely concerned in the formation of the bones of the face, and of those of the upper part and sides of the cranium. The upper and lower jaw bones, the palate bones and vomer, the malar, nasal and lachrymal bones, are included in this category; so also are the frontals and parietals, the squamous part of the temporals, the part of the occipital above the occipital eminence,

and certain slight portions of the sphenoid. In the case of some of the cranial bones thus formed, the precursory membrane is developed outside a corresponding primordial cartilage, which is said to be afterwards absorbed. The cranial bones begin by one or more flat radiating *centres of ossification*, which spread out as the membrane advances, and go on increasing in thickness, until, at length, they meet at the different sutures; after this, they still continue to grow at their edges, until the cranium has reached its full size—an arrangement needed to suit the rapid growth of the brain. The clavicle is likewise in part formed from membrane, but afterwards in cartilage also.

The intra-cartilaginous mode of formation of bone, occurs in the basal portions of the cranium, viz. in the ethmoid, in nearly the whole of the sphenoid, in the petrous and mastoid parts of the temporals, and in the occipital bone below the occipital eminence. It also occurs in all the rest of the skeleton, excepting only the clavicles. For each bone there is developed a separate precursory cartilage, which is enclosed in a definite perichondrium, and is at first small and rudimentary in form, but gradually acquires, as it grows, the general shape of the bone which is to be developed from it. Practically, therefore, the skeleton is, at first, and for a long time, more or less cartilaginous.

Certain *centres of ossification*, one, two, three, or even more, according to the size and form of the future bone, appear at definite spots in the cartilage, and extend into it as the latter increases in size. The cartilage continues to grow in the direction of the articular surfaces of the joints, and also in that of the various processes, until the development of the bone is complete. The bony tissue also goes on growing in the same direction, by the successive formation of the primary and secondary osseous tissue. But in other directions, and especially towards the sides of the bones, the precursory cartilages, sooner or later, cease to grow, and then the further increase in such directions, is accomplished by intra-membranous ossification beneath the soft and growing periosteum.

Suppose in a long bone, for example, a single ossific centre to form in the middle of the precursory cartilaginous shaft, as, indeed, is always the case. Then, separate ossific centres subsequently appear at the ends, constituting what are termed *epiphyses* (*επι* epi, and *φύω* phuo, I grow), and in the larger bones, other smaller pieces are developed at the apices of the more remarkable projections or processes. The precursory cartilage of the bone, at last, ceases to grow in width, and, henceforth, the shaft of the growing bone is steadily increased in diameter, by successive subperiosteal intra-membranous deposits on its outer surface. At the same time, the medullary cavity is formed by a continuous absorption going on within. A platinum wire, placed around the growing humerus or femur of a young pigeon, is found, after a time, enclosed in the substance of the bone, or, if examined a little later, in the hollow of the bone itself. But the precursory cartilage continues to grow in *length* long after, and the bony shaft, and the epiphyses developed at the ends, ultimately meet, but do not coalesce by osseous tissue, until the full length of the bone has been attained. This is evidently a provision for securing a progressive elongation of the bone during many years, together with a proper development of the articular ends of the bones, all

that time. At the ends of the bones, very thin layers of the precursory cartilage, remain permanently unossified, and form the *articular cartilages* of the joints. Immediately beneath this articular cartilage, is a thin stratum of *ossified cartilage* or *primary bone*, recognisable by being smoother and more compact than the rest. This is the only part of the primary bone which is permanent. The rest of this, and, indeed, the earliest formed, and many succeeding portions of the secondary bone, and also the subperiosteal intra-membranous bone, must be completely absorbed, before any long bone has completed its growth; for the young bone would easily lie in what becomes, by continuous absorption, the medullary cavity of the full-grown bone. The mode of increase in long bones, is well shown by giving, at stated intervals, to young pigs or other animals, madder mixed with the food. The colouring matter of this root, has an affinity for the salts of lime, and when it is being taken in the food, the bone then formed has a reddish tinge, whilst the bone deposited at other times, is yellowish white. By this means, it is proved that successive additions are made at the surface and ends of the growing bone, and that absorption of the bone is continually taking place in its interior. Again, the distance between two holes made, one above the other, in a young bone, is not increased by its subsequent growth (Hales, Hunter, Duhamel); whereas a ring of wire placed closely around a growing bone, is soon found to be embedded in its substance, and at later periods, even in the medullary cavity (Duhamel and others).

Most of the smaller bones have but one ossific centre. In the large hip-bones, three primary ossific centres are formed, one each for the ilium, ischium, and os pubis; these grow and finally coalesce around, and at the bottom of, the acetabulum. In the vertebræ generally, three primary ossific centres appear, and then join around the vertebral ring, the bone being afterwards completed by five epiphyses. In both these instances, and also in the case of the occipital foramen, and the cranial cavity, the arrangement described, facilitates the expansion of the cavity or canal, around which the bones are destined to grow. The sternum is formed by the coalescence of many pieces. The cartilages of the ribs, and of the nose, are the unossified parts of the precursory costal and nasal cartilages. Sometimes the number of ossific centres, has reference to the homological relations of the bone.

The order in which the ossific process begins in the various bones of the skeleton, is very singular, not always coinciding with that in which the cartilaginous rudiments of the bones appear. The clavicles are the first bones to show ossific centres, and then the lower jaw, which has one in each lateral half. Next in order, are the vertebræ, the humerus, the femur, the ribs, and the lower and larger portion of the occipital bone. Then, the upper jaw bones, the frontal bone, the scapula, the radius, and ulna, and the tibia and fibula. After that, most of the other cranial and facial bones; the iliac bones, the metacarpus, the metatarsus, and the phalanges of the fingers and toes; the ethmoid, and turbinated bones, the sternum, the ischium and the os pubis; the os calcis, and another of the tarsal bones, named the astragalus, and then the hyoid bone. At birth, and for some time afterwards, all the carpal bones, the five smaller tarsal bones, the last pieces of the coccyx, the patella, and the sesamoid bones, are still entirely cartilaginous, having no ossific centres in them. By

the end of the fifth year, all these, except the scaphoid, trapezoid, and pisiform carpal bones, are ossifying, the last-named bone not showing any ossific deposit until the *twelfth* year. The various epiphyses of the long and other bones, are not all finally joined by osseous union to their respective shafts or chief masses, until after the completion of the full period of growth of the body, or about the twentieth or *twenty-first* year.

The Vertebrate Skeleton generally.—In examining the skeleton of the Vertebrate series of animals, progressive stages of development, from a cartilaginous to a more and more osseous condition, may be recognised. Low in the scale, as in the amphioxus, the skeletal framework is composed of a hyaline substance, containing nucleated cells, between which are very fine fibres. In the Myxinoid fishes, it is composed of very distinct fibres, with cartilage cells intermixed. In the Chimæra, it consists, in some parts, of fibro-cartilage, and, in others, of cartilage. The vertebral column of the sturgeon, is a mixture of cartilage, fibro-cartilage, and bone. In the skates and sharks, the cartilaginous skeleton is covered in parts, or entirely, with a crust of ossific matter. In the Lophius, the bones are fibrous and osseous. Lastly, in the so-called Osseous Fishes, the skeleton is entirely bony.

In the ossified parts of the skeleton of the Cartilaginous Fishes, the bony matter consists either of an irregular granular deposit, between and within the cartilage cells, or of polyhedral bone cells, or of ramified bony laminae. In the less perfectly formed bone, neither lacunæ, canaliculi, laminae, nor Haversian canals exist. In the more complete bone of the Osseous Fishes, those elements are introduced by degrees. The Haversian canals, in some cases, appear as a few long channels, from which simple canaliculi are given off. In a still higher structure, lacunæ, of a peculiar form, are introduced, of moderate size, tapering form, and sending out very short wide canaliculi. Frequently, the lacunæ of different layers of Fishes' bone, cross each other at acute angles; but more commonly, they are arranged in parallel lines. Sometimes no Haversian canals exist; but usually they are present, though small. In rare instances, fine concentric lines are visible around these canals, representing rudimentary laminae. In the lepidosiren, the lacunæ are very large, and the canaliculi much branched; they thus approach the characters of bone in Amphibia.

In Amphibia, the skeleton is entirely osseous; the bony tissue presents large and wide lacunæ, very complex and ramified canaliculi, concentric laminae, and Haversian canals. In a few situations, the lacunæ cross each other at acute angles.

In the Reptiles, and also in Amphibia and Fishes, the bones are solid, or contain but a few recesses filled with fat. The Haversian canals in Reptilian bone are small, the concentric laminae irregular and wavy, the lacunæ of medium size and shorter than in the Fish, and the canaliculi very fine. Some lacunæ cross at acute angles, as in crocodiles.

In Birds, the lacunæ are smaller than in Reptiles, but larger than in Mammalia. In the latter animals, the bony structure resembles that of Man.

Muscular Tissue.

The fibres of both the smooth and the striped varieties of this tissue, have been traced in their development, from nucleated cells, derived immediately from the embryonal cells.

In the case of the *smooth* fibres, the nucleated cells, at first roundish, become elongated and fusiform; their cell walls and their contents blend into one mass, which assumes, by degrees, the sarcoous character; in the meantime, the nucleus of each fusiform cell, becomes much elongated. Many such fusiform cells produce, by their cohesion, a smooth muscular band.

The *striped* muscular fibres have been described, by some, as arising, each from the coalescence of rows of nucleated cells (Schwann). But by other and more recent authorities, they are regarded as being each developed by the extreme growth of a single cell (Remak, Fox). It has also been maintained that they originate without the intervention of true cells, through the agency of rows of nuclei, lying in a blastema, which afterwards gives rise to the fibre, by a series of changes occurring in it (Savory). These differences of opinion are probably as much due to the different interpretation of the same appearances by different observers, as to differences in the observations themselves. They illustrate the difficulties of microscopic research. If the primitive animal cell which forms a muscular fibre, be regarded as a gymnoplast, easily fused with its neighbours, the discrepancy of opinion may, perhaps, be reconciled.

Supposing rows of nucleated cells to coalesce, to form a single fibre, it is believed that the coalescing parts of the cell walls, are absorbed, and that thus a long tube is formed, which ultimately becomes the sarcolemma; the contents of the united cells, at first finely granular, are said to grow and become sarcoous, their elements arranging themselves into linear and transverse series, first on the outer surface next to the sarcolemma, and then more centrally, so as to form the transversely marked fibrillæ. In the meantime, as the cells grow in length, the nuclei separate from each other, and become obscured, but are never lost. If, however, only one long cell forms each fibre, the wall of such an elongated cell, is believed to constitute the sarcolemma, and the contents, originally granular, are said to be gradually increased and differentiated into the fibrillæ, first becoming marked by longitudinal lines, and afterwards by transverse striæ. The nuclei multiply by successive subdivisions, and remain surrounded by granular matter. By many, it is thought that the original cell wall, or cell walls, do not form the sarcolemma, but that this is the result of a subsequent deposit of homogeneous membrane around the nearly perfectly formed bundle of fibrillæ.

Whatever their precise mode of origin may be, the muscular fibres seem, when first recognisable, like very fine bands, sometimes not more than one-tenth of the diameter of the fully formed fibre, and having bulging nuclei in them at intervals. When composed of such fibres, the young muscles resemble their tendons. As the fibres gradually increase in width, they assume the adult characters, and become uniform in diameter, so that the nuclei are no longer so easily visible (fig. 122, *g*). At birth, all the muscles are said already to contain their full number of fibres, so that their future growth consists only in an increase of length and width

of the pre-existing fibres. At birth, the fibres are about one-fifth of their ultimate dimensions. The fibrillæ of each fibre, may during growth become a little wider; but it is thought rather that they increase in number. In other words, the individual sarcous elements retain their size, but they are accumulated in a greater number of longitudinal rows. In the enlargement of the muscles, which takes place from exercise, in all probability the fibres do not increase in number, but in size, and contain either more or larger fibrillæ. In the opposite condition of the wasting of a muscle, the fibres remain the same in number, but become smaller, owing to a diminution of their contents; the fibrillæ also decrease in number, grow indistinct, or even disappear altogether. In a wholly paralysed, unused, or diseased muscle, fatty matter is substituted for the characteristic sarcous elements.

It is obvious that such striped muscular fibres as, like those of the heart, are but indistinctly striated, may be regarded as less perfectly developed fibres. Certain of the smooth fibres, in which the sarcous elements are very distinctly granular, or dotted, also approach in character and development, to the higher or striated form of fibre. The fusiform fibre cells, and last of all, the elongated, spindle-shaped, oval, or round contractile cells of the heart of the embryo, are the lowest form of all. There is thus a gradual transition from the simplest to the most complex form of muscle cells.

In the case of the ramified form of the striated muscular fibre, noticed in the tongue, lips, and face, and of the reticular form observed in the walls of the adult heart, the primitive nucleated cells, out of which they are developed, either simply ramify, or ramify and coalesce with the branches of other cells, and then acquire their sarcous contents.

Nervous Tissue.

The *ganglionic cells*, fig. 122, *b*, are derived from metamorphosed embryo-cells, and from the direct descendants of those cells, by ordinary modes of multiplication. The rounded ganglionic cells are formed by a simple enlargement, and a gradual alteration of their contents; the nuclei persist, and are very distinct; the branched cells are formed by the outgrowth of one or more of the peculiar processes with which they are provided. The envelope is prolonged on to the processes, and becomes connected with the homogeneous tubules of the nerve fibres; the processes contain nervous substance. The very small rounded cells, and the free nuclei, found in some parts of the grey substance of the nervous centres, may be early stages of future ganglionic cells.

The *grey or gelatinous* fibres, found chiefly in the sympathetic system, whether they be regarded as true nervous elements, or as a peculiar form of connective tissue cells, appear to be produced by the coalescence of elongating fusiform nucleated cells, the contents of which, as the cells enlarge, become soft and finely granular, whilst the nuclei appear wider and wider apart. Even in the most highly developed of these fibres, there is but little evidence of a tubular character or wall. The medullary sheath or fatty layer is absent. They have been compared, by some writers, to the non-medullated portions of the white nerve fibres, or to the axis cylinder or central band only of those fibres, which, however, have a tubular sheath. The most perfect grey fibres cer-

tainly resemble a transitory condition of the fibres out of which the white or tubular nerve fibres are developed.

The *white* dark-bordered, or double contoured *tubular fibres*, are themselves derived from fusiform nucleated cells, which are embryo cells, or their descendants. By coalescing, they first form grey granular fibres, with elongated nuclei at intervals, and, in that stage, resemble the grey or gelatinous fibres of the sympathetic system. But the greyish contents of these fibres, soon become opaque and white, and resolve themselves into the central albuminoid band or axis cylinder, and then acquire the surrounding fatty layer or medullary sheath; whilst the walls of the coalesced cells, are said to unite, to form the outer tubular membranous sheath of the perfect fibre. Instead of imagining many cells to coalesce, a single cell may be supposed to go on dividing, to form a nerve fibre.

The branched terminations of the nerves, according to what has been seen in the tadpole, originate in the junction of ramified formative cells, which keep on joining those already further developed.

Sometimes more than one white tubular fibre has been seen forming in a single embryonic, or less developed, one—a fact which would show that the tubular membranous sheath might be developed otherwise than by the cell walls of coalesced formative cells.

Bloodvessels.

The arteries and veins, excepting the very finest, are, as already mentioned, not so much tissues as compound structures, built up of several tissues. They are developed in two very different ways.

In the first place, the principal vascular trunks, or the *arteries* and *veins*, of the germinal membrane of the embryo generally, and of its commencing organs, and indeed the *heart* itself, appear primitively as solid cords, composed of multitudes of embryonic nucleated cells. After a time, the innermost part or axis of these cords, becomes changed into blood, the soft spaces coalescing and forming a system of canals; whilst the outermost cells are then gradually metamorphosed, in the ordinary manner, into the epithelial, elastic, muscular, and connective tissues which compose the coats of the vessels. This mode of formation is apparently limited to the early and principal vessels; for subsequently, the arteries and veins, which are continuously being added, as the body grows, are developed in another manner—viz. by the transformation of previously constructed large-sized capillaries, the calibre of which is increased, whilst the coats are gradually thickened, by the formation of additional tissues developed in the ordinary way.

The capillary vessels originate in two modes, according to their size. The larger *capillaries* are formed by the coalescence of linear series of nucleated cells, and the subsequent absorption of their attached ends, so that a homogeneous tube is produced, recently shown to be lined with a fusiform epithelium, the nuclei of which seem to be attached to the walls of the vessels. These soon become connected with previously existing vessels, and the blood then enters them. The finer vessels, or those of the actual *capillary networks*, originate in nucleated formative cells, lying amongst the elements of a newly growing tissue; these become ramified or stellate, by sending out fine processes or branches, which run towards, meet, and coalesce with, other fine processes growing from

the larger capillaries just described ; afterwards they coalesce with processes of other ramifying cells which appear in succession. These coalesced processes and the cells themselves, become progressively enlarged and hollowed out, so that a tubular or vascular network is produced, the component vessels of which, though, at first, so fine as to convey only the liquor sanguinis or plasma of the blood, become ultimately wide enough to carry the blood corpuscles also (fig. 122, *h*). New capillaries may also be developed within the meshes formed by the older ones. The walls of the coalesced ramified cells, constitute the homogeneous membrane of the coats of the capillaries, in which the nuclei of the formative cells, and especially those of the epithelial lining afterwards formed, can be recognised. The more numerous and closely set the stellate formative cells, the closer is the capillary network developed from them.

Blood.

This important fluid is primitively developed, as already mentioned, in the interior of the newly forming heart and principal vascular trunks. At first, its structural elements—the *blood-cells or corpuscles*, are colourless cells with faintly granular contents and a distinct nucleus, in all respects identical with the embryonic cells. They soon become loosened, and then separated from each other, by the formation of an intermediate fluid plasma, the new *liquor sanguinis* ; their contents become less granular, and coloured by the formation of colouring matter in their interior, but their nucleus remains. They are now red blood-corpuscles ; but as compared with those of the fully formed blood, they are much larger, spherical instead of discoid, darker in colour, and *nucleated*, instead of being destitute of a nucleus. Once formed, they speedily enlarge, elongate, or assume a somewhat flattened and elliptical figure, somewhat resembling the shape of the blood corpuscles of the Amphibia ; the nucleus soon divides into two, or even into three or four portions, or young nuclei ; the walls of the so altered cells, then become constricted between these young nuclei, and, ultimately, the cells divide into as many new cells as there were nuclei ; this process, it is supposed, may be repeated over and over again.

After a time, corresponding with the date at which the liver begins to grow, this process of subdivision of the primitive nucleated red-corpuscles ceases, and then multitudes of colourless nucleated cells appear, especially in the blood of the liver and of the spleen, and also in the lymphatic system ; and either without, or with, previous multiplication by subdivision of their nuclei, constriction of the cell wall, and actual partition, they acquire, even within the spleen and liver, some red colouring matter, and are changed into *nucleated* red-corpuscles.

Both sets of these spherical, nucleated red-corpuscles, are ultimately converted, by a slight diminution of size, by a flattening of two opposite sides, and by the gradual wasting and final disappearance of the nucleus, into the typical *non-nucleated* disc-like red-corpuscles of the fully formed blood. This condition exists at, or even a considerable time before, birth. After birth, during the growth of the body, and in the adult, the red-corpuscles of the blood are developed from the colourless ones, as already elsewhere described (p. 315).

The *white* blood-corpuscles are evidently the unaltered, colourless,

nucleated cells, derived, at first, from the blood itself, afterwards from the liver, and permanently from the spleen and the lymphatic system. Under certain circumstances, as in inflammation, colourless blood corpuscles may perhaps originate in the blood itself, within the general capillary system.

The *plasma* of the blood, at first the product of the liquefaction of the intermediate blastema or matrix, probably effected under the agency of the formative cells, is afterwards the complex result of various acts not only of a formative, but also of an absorptive and excretory kind.

Lymphatics or Absorbents.

The mode of formation of the principal absorbent trunk, the thoracic duct, is probably like that of the primitive bloodvessels.

The small *lymphatics*, according to observations made in the tadpole's tail, originate by the junction of nucleated cells, in the same way as the large capillaries; but they are said to anastomose much less frequently. The extension of the absorbents into newly growing tissues, is effected, as in the case of the capillary network, by the formation in the new tissue, of peculiar cells, which branch out, and join certain very fine processes, given off from the lymphatics already developed. These stellate cells are said to be more jagged in their outline, than those of the capillaries.

The lymphatic *glands* are believed to be developed from clusters of lymphatic vessels, which give out projections, afterwards converted into the alveoli or cells of the cortical portion of those glands.

The chief microscopic structural elements of the lymph and chyle, the small and large nucleated *corpuscles*, most probably originate in the lymphatic vessels and glands, by subdivision of pre-existing corpuscles, and perhaps multiply by subdivision. Probably also some of those seen in the chyle and intestinal lymph, before it reaches the mesenteric glands, originate in the solitary or agminated glands. They also seem to be formed in the spleen, thyroid, and thymus glands, or even in the interior of the commencing lymphatics. At first, these cells are minute, and their envelope closely surrounds the nucleus. In this form, they constitute the small lymph corpuscles. They grow into the larger ones, by the deposition of soft granular matter between the exterior and the nucleus. They also multiply by elongation, subdivision of the nucleus, constriction of the delicate cell-substance, and partition into two new cells, each having its own nucleus.

The molecular base of the chyle, is apparently the result of a process of aggregation of the simplest kind, whilst the fluid part of the lymph and chyle, may be regarded as an extremely diffuent blastema or fluid matrix.

Vascular or Ductless Glands.

The several organs thus grouped together, arise from masses of primitive embryonic cells and blastema, which appear in the situations already described with their development as organs. The closed sacs of the lingual, tonsillar, pharyngeal, gastric, and solitary and agminated intestinal glands, and also the closed sacs or Malpighian corpuscles

of the spleen, are developed by the multiplication of cells or cell-nuclei, of which the outer ones form a membranous envelope, and the inner ones the special pulp, with its traversing bloodvessels. The cells of the thyroid body, and those of the supra-renal body, originate also by cell-growth, which is most readily observed in these peculiar organs. The new cells of the thyroid are said to be formed by a process of budding or protrusion, and subsequent constriction and separation. The parenchyma of the spleen, the thick walls of the recesses of the thymus, as well as its fluid contents, and lastly the pituitary body, are formed of gymnoplasmata, nuclei, and a matrix.

Secreting Membranes and Glands.

The subcutaneous synovial bursæ, mere interspaces in the subcutaneous connective tissue, probably arise, at first, by a process of softening and absorption of that tissue, and afterwards by an extension of their walls. In the true synovial membranes, in the serous membranes, and in the mucous membranes, the defined *limiting* or *basement* membrane is developed from very fine, almost homogeneous, connective tissue; but in the glands, the well-defined *glassy basement* membrane is supposed to be a sort of excretion from the epithelial cells which cover the surface. The origin of the glands, as organs, has already been described. They commence as masses of nucleated cells, evidently destined to be epithelial; these project into, and fill up, recesses in the corium beneath. They either remain simple, as in the case of the gastric tubuli, or they may extend so as to develop the most complex gland, like the liver or kidney. The cavities of the ducts, which are at first solid, are formed by a softening of the intercellular matrix, along certain special lines of cells.

Epithelial and Epidermoid Tissues.

These arise, generally, from the multiplication and metamorphosis of the embryonic cells of the outer and inner germinal layers of the embryo. In the case of the serous membranes and of the synovial membranes of the joints, they also originate from cells in deeper portions of the embryonic structure.

The modifications which these cells undergo, however various, always permit them to retain their nucleated-cell character throughout their whole existence. The changes of shape, structure, and contents, necessary to transform them into the various kinds of *epithelial* and *epidermoid* structures, can be understood by perusing the description of them in vol. i., p. 72. Pigmentary deposits may occur either in simple epithelial cells (fig. 43), or in ramified cells (fig. 122, f).

In the many-layered epithelia, these changes may be seen at one view, all occurring simultaneously (fig. 44). The cuticle at first cannot be distinguished from the cutis. All the epithelia, as well as the epidermis, exhibit a continuous growth. The glandular epithelia show the widest departure from the primitive cell-type, especially as regards the chemical composition of their contents. The mode in which cilia are developed on the ciliated epithelia, is not exactly known. It may be by outgrowths of the cell-wall, including processes of the cell-contents, or by a fission of the substance of the cell.

The *nails* are developed, not on the surface, but beneath a thin epi-

dermic covering; the young nail consists of compressed and easily separable cells.

The *hairs* appear as little black specks under the cuticle; these are clusters of coloured epidermic cells of the Malpighian layer, fitting into depressions in the cutis, which are lined by a basement membrane. This rudimentary follicle enlarges, and acquires its flask-shaped character; its walls are formed by the thickened basement membrane, and by a layer of cells, belonging to the corium, outside it. The outer epidermic cells form the root-sheaths, and the central ones, resting upon a little vascular papilla, develop into the hair. This increases in diameter and length, and then pierces the cuticle, beneath which it is really formed, sometimes by its point, and sometimes in a bent position. The first hairs are very fine, and form the down or *lanugo*. All new hairs, when old ones are to be shed, commence by a cluster of epidermic cells, formed at the bottom of the hair-follicle, upon the side of the old papilla; as these grow, they detach the old and falling hairs.

Dental Tissues.

The *dentine* is a *dermoid bone*, formed by the gradual transformation and ossification of the superficial portion of the dental papillæ or pulps, and not by a mere excretion or deposit on their surface. The pulp is chiefly composed of rounded nucleated cells, in a clear matrix, but contains also a few areolar fibres, and many bloodvessels. The outer cells become lengthened, like columnar epithelial cells. By some, it is thought that a single layer of these cells, may, by elongation and other modifications, develop into the whole length of a dentinal tubule. It is more commonly supposed, that successive layers of pulp-cells are developed, coalesce with each other, undergo metamorphosis, and become ossified, in order to complete a tubule. Lastly, it has been suggested, that rows of secondary cells developed within one primary cell, and subsequently coalescing, are so transformed. There are differences of statement, as to the mode in which this occurs. The nuclei of these secondary cells, are supposed to coalesce, and, remaining hollow, to form the dentinal tubuli. All the other parts of the cells, and of the intermediate matrix, become calcified, and constitute the walls of the tubuli and the intertubular dentinal substance. The fine bifurcated ends of the tubuli, are formed by branching and anastomosing processes of the cells. Upon the surface of the growing dentine, next to the enamel, is seen a fine basement membrane, named the *preformative membrane*; it is supposed to be the seat of commencing calcification, to be very early converted into the more compact superficial dentine, and to assist in connecting this with the enamel.

The *enamel* organ (p. 625) consists of a soft pellucid tissue, entirely epithelial in its nature. It is composed, on its inner or deeper aspect, of a layer of columnar epithelial cells, which are applied to the preformative membrane of the dentine. Outside these, is a thick stratum, composed of stellate cells, forming a network of fibres, enclosing multangular areolæ, filled with transparent substance, and having brilliant spots at the junctions of the fibres. Its outer part consists of epithelial cells, arranged in masses, between projections of the enclosing vascular mucous membrane. These masses are sometimes so large and prominent,

as to appear like white bodies beneath the gum, and have been erroneously regarded as glands—the *dental glands* (Serres). It is usually stated that the cells of the enamel organ, become elongated, and calcified, with gradual absorption of their animal substance—at first forming a soft cretaceous mass, but afterwards becoming hard, and being firmly fixed to the surface of the preformative membrane (Schwann, Kölliker, and others). Their nuclei disappear, or leave only a fine linear trace. It has been supposed that the enamel-cells are developed beneath the preformative membrane (Huxley); but this view is not generally entertained. It is variously imagined that a single prismatic cell serves to form a single enamel prism, running through the whole thickness of that structure; or that several secondary cells combine to form each prism. As the enamel organ terminates at the cervix of the tooth, the formation of enamel is limited to the crown. The *crusta petrosa* is developed upon the fang, probably by intra-membranous ossification.

REPARATION.

The process by which injured or lost parts of the body, are repaired or reproduced, so that similar tissues are, after a time, developed in their place, is known as *regeneration* or *reparation*. The formative power is here the same as that by which the embryo is first developed, and the developmental processes concerned, are but extensions of those retained in mature life. This process of regeneration is most active during the earlier periods of existence. Thus, in cases of so-called spontaneous amputation occurring to the fœtus in utero from constriction by the umbilical cord, fingers have been afterwards developed on the remaining portion of the limb. Instances, too, have been recorded, in which almost as remarkable re-formations of lost parts, have occurred in infants, and even in children. In the same manner, the capacity of repair gradually diminishes as life advances, lost parts which, in early life, are regenerated, being afterwards imperfectly and incompletely re-formed. Hence, in a child, the reparation of an injury may easily take place; whereas in old age, a similar lesion will remain unrepaired. Experiments have shown that the vigour and celerity of the repair of fractures, and the union of tendons in Mammalia, are in an inverse proportion to the age of the animal (Paget).

Amongst the lowest animals, the process of reparation after injury, is identical with the process of reproduction by gemmation or fission. If the hydra be cut up into a number of small pieces, each of these becomes developed into a perfect hydra, and this process can be repeated, over and over again, with a similar result. The Annuloida likewise possess very great reparative powers; thus it has been noticed that the holothurida, when pulled about or injured, expel the whole of their viscera; after a

few months these are regenerated. Amongst the higher Nonvertebrate animals, however, in which reproduction by gemination or fission does not occur, the power of reproducing a perfect body from a fragment does not exist. The Crustacea and Arachnida can, when fully developed, reproduce limbs and antennæ. In the Myriapoda, on the other hand, the reparative power ceases when they have reached their full development; whereas, previously to this, antennæ and limbs may be reproduced. The larvæ of Insects are endowed with like powers of reproduction; but the perfect Insects, at least the higher ones, have no such regenerative power. Hence it appears that the amount of reparative power, is in an inverse ratio to that of the development through which the animal has passed in its attainment of perfection (Paget). The reproductive power of the Mollusca has not been much investigated; it is said that the common snail can reproduce the head, if the cerebral ganglion be preserved. Amongst the Vertebrata, the Amphibia possess very great reparative power. After excision of an eye from the triton, or newt, a new one, it is said, may be developed in its place, and the reproduction of an entire limb, or of the tail, occurs readily in them.

But in Man and the Warm-blooded animals, the true reparative process is much more limited, being confined strictly to the reproduction of certain tissues.

In the first place, there are several parts, such as the epidermoid and epithelial tissues, and also the red corpuscles of the blood, which are naturally undergoing constant reparation or decay, and are as constantly being reproduced, by what has been termed *continuous growth*, or *nutritive repetition*.

Secondly, certain tissues of comparatively simple structure and chemical composition, and of low vital endowments, appear to be capable of regeneration. Such are the areolar and fibrous tissues, elastic tissue, and bone, which fulfil mechanical uses in the body, serving to connect and support its various parts.

Lastly, bloodvessels, lymphatics, and nerves, tissues which penetrate other parts or organs, are likewise endowed with this power.

Other tissues and organs of a special kind, which have a complex structure, higher chemical constitution, or peculiar properties or functions—such as true cartilage, muscle, the grey substance of the nervous centres, the essential parts of the organs of special sensation, the cutis and its glands, the secreting and excreting glands, and the ductless glands—are not regenerated after injury or destruction.

The regeneration of particular tissues, is accomplished by the multiplication and evolution of previously formed cell-elements, whether these be gymnoplasts, nuclei, or nucleoli; and by the modification of the intercellular or internuclear

elements, or matrix, within the sphere of action of those nutritive centres. In this way, the *epidermis* and *epithelium* are speedily reproduced. The mode of formation of new *lymph-corpuscles* and *blood-corpuscles*, already described (p. 657), is to be explained in a similar way. The *connective*, membranous, fibrous, or tendinous areolar tissues, and the elastic tissues, are regenerated in the same manner as that in which they are developed. Connective tissue is the chief medium of restoration or repair in wounds or ulcers of tissues or parts, which, like muscles, glands, and the cutis, are not reproduced. In its growth, it becomes penetrated by new capillaries and lymphatics, which are developed after the manner already described as their original mode of formation. The development of *new vessels*, in the meshes of effused lymph or blood, in the restoration of the lost tail or limbs of the *Amphibia*, and also in tumours, is accomplished in the same way. *Cartilage* if removed by accident, or softened and absorbed in disease, is not regenerated, but cup-shaped cavities are left, which may wear smooth; if it be rent or broken across, it does not unite, but the separated parts become connected by strong fibrous or osseous belts. New cartilage is produced in certain tumours. *Bony tissue* is regenerated with remarkable facility; the process always takes place by the intra-membranous form of ossification. The intra-cartilaginous form, however, occurs in tumours. Injury to a *muscle*, such as division of its fibres, provided that the cut ends have not retracted too far from each other, is repaired by a uniting band of dense connective tissue, which re-establishes the continuity and office of the muscle; but when a whole muscle is torn across, it may retract, and form altogether new connections, or it may cease to be used, and then undergo fatty degeneration. A divided *nerve* is quickly united by connective tissue; in the cicatrix, nerve-fibres are afterwards formed, which join the divided fibres, and completely restore their functions, whether these be reflex, sensory, or motor. The nerve-fibres beyond the line of section, usually lose their medullary substance or sheath, which previously undergoes a granular and fatty degeneration; but the tubular sheath, the axis-fibre, and the nuclei remain. When the ends of the nerve are once more united, the medullary sheath of the fibres is reformed, the reproductive process beginning at the cicatrix and extending downwards. In young animals, the medullary substance may be restored before the nerve is united.

GROWTH.

The human infant, especially, exhibits an imperfect and feeble condition at birth, and many changes, besides mere increase of size, take place in it, before it reaches the conditions of puberty and maturity. At birth, the average weight of the male infant is about 7lbs., and of the female infant about 6½lbs. The lengths, in the two sexes, are about 18½ inches and 18 inches. The nutritive vegetative functions alone exhibit a special activity, those of animal life proper being comparatively quiescent. The new-born child takes food, and sleeps; at first, it passes upwards of twenty hours out of the twenty-four, in a state of slumber; and during the first year, it requires from twelve to fifteen hours' repose. The respiration, circulation, and development of heat are relatively more active than in the adult; but the power of resisting cold is feeble, and hence protective clothing is necessary.

The general growth of the body, is at first rapid, but afterwards much more gradual. Half the adult height is reached by about the end of the third year, whilst to attain the remaining half, fifteen or eighteen years more are required. At 20 years of age, a Man is rather more than 3½ times his height, and about 20 times his weight, at birth. This growth is not equal in all parts of the body, the lower extremities, which were less developed in the embryo, now becoming proportionally more developed: on the other hand, not only the head, but also many internal organs, such as the liver, kidneys, and supra-renal bodies, which are proportionally large at birth, afterwards grow relatively more slowly; the thymus gland even shrinks. The muscular system and the volitional power which commands it, are simultaneously developed and strengthened. At the end of the third month, the infant easily supports the weight of its head; at the fourth month, it is able to sit upright; at the ninth month, it crawls on the ground; before the end of a year, it can, with assistance, step; and at various times, from one to two years or more, it can stand, and begin to run alone. At six months, it can lisp, and, before the end of the year, can imitate a few definite articulate sounds of one or two syllables. The senses and the mind are gradually brought into exercise, hearing, as indicated by the effect of noises, before sight, as shown by the attractiveness of light or of bright-coloured objects. The development of sight, as a source of definite knowledge, under the education of touch, has

been already fully explained. Of the other senses, perhaps, taste is the next to be developed, and after that, smell and touch. The order of appearance of the milk and permanent teeth, has already been detailed. The food of the infant, before it acquires teeth, is fluid, and the entrance of this into the stomach, distends that organ, and completes its transverse direction; after the teeth appear, the food may be increased in density, from semifluid to more or less solid nutrient substances.

Life has been divided into periods, which may be physiologically thus distinguished. From birth to the appearance of the first tooth, the child or infant may be called a *suckling*; from thence to the time when the milk-teeth begin to fall out, is the period of *childhood*; thence to the period of puberty, is the age of *boyhood* or *girlhood*; from this to the final completion of the stature, is the epoch of *youth* or *maidenhood*; after that, is the period of *maturity*. Beyond this, comes the *decline of life*, and afterwards *old age*.

Puberty occurs in the male, at the age of from fifteen to eighteen, according to the climate, and in the female, from twelve to fifteen. After the full stature has been attained, a certain development still goes on, the skeleton especially strengthening and solidifying itself, even up to the age of 25 in women, and 28 or more in men. At this period, also, the intellectual powers attain perfection, and the balance between assimilation and waste, is fully established.

DECAY AND DEATH.

The life of every organised being, depends ultimately on the due and persistent performance of the tissue-changes. These are not only constantly wasting and undergoing repair, through the whole organism, by which means the life of the individual is maintained, but they degenerate and decay. Their nutritive energy becomes enfeebled; they are no longer renewed or repaired; their further development is arrested; the organs no longer perform their various functions; and then natural decline, *decay*, and finally *death* ensue.

Death may affect a tissue, or a part, or an organ only, of the body; it is accordingly said to be *molecular*, or *partial*, as the case may be; this is illustrated in *ulceration*, and *gangrene* or *mortification*, of the soft tissues, or *caries*, or *necrosis*, of bone. General death, also called *somatic death* (ζῶμα, the body), affects the entire system. Partial or molecular death is

only followed by general or somatic death, when it interferes with the processes of organic life. Somatic death is the result of a permanent arrest of the circulation. Besides this *natural* mode of death, or death from *old age*, or *climacteric* death, there are *unnatural*, *premature*, or *accidental* modes of death, which may occur at any period or moment. The immediate causes of accidental or unnatural somatic death, are *syncope*, *asphyxia* and *coma*; these occur from injury or disease. Old age is the cause of natural somatic death. Coma and syncope have been alluded to in the Section on the Nervous System, vol. i. pp. 296, 355; and asphyxia is described at length under Respiration, vol. ii. p. 473. They may here be again briefly noticed.

In *syncope*, death begins at the heart, this organ either losing its irritability and power of contractility, or being affected with a tonic spasm. In the former case, it is found, after death, flabby and flaccid, with its cavities either filled with blood, or empty; in the latter case, it is firm and contracted, and almost or entirely empty. Death by syncope, may be occasioned by widely different causes. Thus, it may take place through the nervous system, as when a violent shock or concussion is communicated to the body; it is in this mode, that strong mental emotion, as intense fear, joy, or grief, or sunstroke, lightning, extensive burns of the surface of the body, and sedative poisons, are fatal to life. The effects of many sedative poisons—as, *e.g.* of aconite, digitalis, and tobacco—are produced by the passage of the deleterious substance into the blood, and by the action of the blood, thus vitiated, on the nerves of the heart. Again, death by syncope may proceed from an enfeebled condition of the heart's substance, so that its contractile power gradually fails, a mode of death which is exceedingly common. It occurs in persons affected with disease of the tissues of the heart, especially in cases of fatty degeneration of this organ. Starvation (p. 549), exhausting diseases, and long-continued violent exertion, are further causes of death from feebleness of the heart's action. Lastly, this mode of death may occur from sudden and profuse hemorrhage, the circulation being arrested, not from loss of the contractile power of the heart, but owing to the insufficient quantity of blood which passes into its cavities. It takes place when a large bloodvessel is wounded, or when it is ruptured owing to disease of its coats, and in cases of profuse internal hemorrhage, as when an aneurism bursts.

Death by *asphyxia*, or suffocation, occurs when the move-

ments of respiration, or the access of oxygen to the lungs, are arrested, the flow of blood through the pulmonary capillaries then ceasing. This mode of death occurs in cases of disease affecting the heart and lungs, and, though more rapidly, in choking, strangulation, and drowning. The breathing of carbonic acid and other poisonous gases, also kills by asphyxia; but this fatal result is due both to the absence of free oxygen and to the deleterious properties of the gas. The simple privation of atmospheric air, acts only indirectly on the heart; for the movements of this organ, and, indeed, even the pulsation of the smaller arteries, continue for a time, although all other signs of vitality have disappeared. The blood, as it traverses the pulmonary capillaries, now no longer undergoes the chemical changes essential to respiration, for it is non-aërated or venous, and cannot therefore sustain the functions of the various parts to which it is distributed. At first, it passes freely through the pulmonary veins to the left side of the heart, whence it is distributed through the arteries, to the different parts of the body. Its noxious action on the brain, is quickly shown, by the rapid suspension of its sensorial functions, unconsciousness, and convulsions. The circulation in the pulmonary capillaries is at first gradually retarded, and at length totally arrested; so that the lungs are gorged, and the right side of the heart over-distended with venous blood, which passes into the left cavities of the heart, in smaller and smaller quantities. Owing to this diminution in the supply of blood, and to its vitiated quality, the contractions of the heart become gradually more feeble, and finally all the vital actions are arrested. In the first stage of asphyxia, the face is livid, although voluntary, or instinctive and conscious, efforts are made to breathe, but without success. In the second stage, volition and even consciousness are lost, though convulsive movements are performed. In the third stage, all outward and respiratory movements have ceased, but the heart still beats. In an asphyxiated animal, the heart will beat for seven minutes, or three minutes after the arrest of external movements.

In *coma*, death begins at the brain, the sensorial functions being those which are first suspended. This mode of death occurs in fevers, in certain diseases of the brain, and in injuries of this organ, when these do not kill by shock or concussion. Thus, a person may receive a violent blow on the head, giving rise to symptoms of syncope; and after a time, although the heart regains its power, and respiration and circulation still

continue, a state of profound stupor sets in, and death occurs in a comatose condition. Narcotic poisons, such as opium, belladonna, and chloroform, also produce death by inducing coma.

Death, however, frequently occurs in all these three modes. Thus, pressure on the brain, may not only induce coma, but also asphyxia and syncope, by paralysing the medulla oblongata, from which the pneumogastric nerves, supplying the heart and lungs, arise. The fatal effects of chloroform, on the other hand, may depend on asphyxia, coma, or cardiac syncope.

Death from *old age*, or the *gradual decay of nature*, the natural mode of dying, is much less common than death from unnatural causes. Towards the decline of life, the formative power becomes defective; the processes of nutrition, growth, and development of the tissue elements, no longer keep pace with the individual waste and death of these; so that the various organs of the body suffer a marked and gradually increasing structural deterioration or *degeneration*, and their functional powers are consequently diminished. These deteriorations or degenerations constitute *senile atrophy*, and are as natural and normal to the living organism as nutrition itself. The body either wastes and dries, or it grows fat, the individual either becoming emaciated or else corpulent. The coats of the arteries undergo fatty changes, the cornea exhibits the *arcus senilis*, and there is an increased quantity of fat in all the tissues and organs. The arteries become the seat of calcareous deposits, the bones contain an increased quantity of earthy salts, and the cartilages undergo ossification. The walls of the bloodvessels and other structures become thickened; the mucous membrane of the alimentary canal frequently presents an ash-coloured appearance, and the lungs, even early, exhibit deposits of black pigment. Lastly, if disease or injury in no way interferes with the ordinary duration of life, the activity of all the functions slowly diminishes, until the vitality of the entire organism gradually becomes extinct.

The ordinary external appearances which indicate death, are, the cessation of breathing, the absence of pulse, a half-closed state of the eyelids with dilatation of the pupils, clenching of the jaws with slight protrusion of the tongue, and partial contraction of the fingers. The skin is cold and pale, or, if livid, is becoming paler. After a few days, a deceptive increase of colour of the skin, is sometimes noticed, owing to the blood being forced, by the evolution of gases from the larger central vessels, into the small vessels of the skin.

The only positive *signs* of *actual* death are those which depend on molecular change or death, viz. *rigidity* of the muscles of the whole body, and *putrefaction* of the tissues. These are most marked in organs and tissues, the vital functions of which are the most active. They supervene more rapidly in Warm- than in Cold-blooded animals. The action of the heart and the movements of respiration, may be so much reduced, as to be altogether imperceptible, so that the functions of circulation and respiration, appear to be arrested. This is occasionally observed in temporary syncope, in which a person, to all appearances dead, has, after a time, regained consciousness, and recovered. The peculiar condition of the nervous system called *catalepsy*, and the state of *trance*, are likewise further examples of so-called *apparent* death. But, as previously stated (vol. i. p. 163), on the occurrence of actual death, the irritability of the muscles, by degrees, disappears, electricity no longer excites their contraction, and then cadaveric *rigidity* sets in. The time at which this comes on, its duration, and many other points connected with it, have also been there mentioned. The commencement of *putrefaction* is first indicated by the appearance of a bluish-green patch on the surface of the abdomen or thorax; this goes on increasing in size, and becomes brownish, the margins by which it spreads, retaining, however, the primitive colour. Putrefaction then shows itself in other parts of the body. The rapidity of this process, presents great differences, the tissues being much more prone to putrefy after certain diseases; the temperature of the surrounding air, also influences, considerably, the quickness with which the dead body is finally decomposed.

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LONDON

PRINTED BY SPOTTISWOODE AND CO.

NEW-STREET SQUARE

